Systematics and phylogeny of the ant-eating spiders (Araneae ; Zodariidae) : a total evidence analysis

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This PhD thesis mainly aims at the systematic revision of the ant-eating spiders (Zodariidae) using a combined phylogenetic approach. Initially, taxonomic description of several new zodariid taxa was carried out to document significant structures that had not been observed in spiders so far. As a result, a novel zodariid synapomorphy was discovered while describing the new genus *Palindroma* and a double femoral gland was revealed in the new genera *Suffrica* and *Suffascar*. Ultimately, a phylogenetic study on a global scale was undertaken, based on the largest taxonomic sample of Zodariidae analyzed to date. The character matrix comprised 153 morphological features spread over 11 structural groups and the molecular data included 5 genetic markers (1 mitochondrial and 4 nuclear markers). Different phylogenetic analyses were performed based on morphological, genetic and combined datasets. The results revealed 5 groups corresponding to 5 sub-families. As predicted, the Cyriocteinae appear sister to all other Zodariidae. The Lachesaninae, Cryptothelinae and the Zodariinae were redefined. The Storenomorphinae appeared paraphyletic in the molecular and combined analyses and fell into the Cryptothelinae. As a consequence, Storenomorphinae were fused into the Cryptothelinae. The Storeninae were re-established and redefined. *Procydrela procursor* could not be assigned to any subfamily and it may be considered to put it in a group of its own.

Arnaud Henrard was born in Ostend (Belgium), on May 17th, 1983. He spent his childhood in RD Congo in Africa, where his interest in nature, especially in the smallest bugs, emerged. Logically, he studied biological sciences at the Université catholique de Louvain (Belgium) and, in 2009, he obtained his Master degree in Biology of Organisms and Ecology with high mention. His encounter with his mentor Rudy Jocqué plunged him into the world of spiders and, during his PhD thesis, he mainly worked at the Royal Museum for Central Africa.

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« Le hasard est une toile d'araignée dans laquelle le destin peut parfois se prendre »

– Maxence Fermine, Opium (2002)

SYSTEMATICS AND PHYLOGENY OF THE ANT-EATING SPIDERS (ARANEAE; ZODARIIDAE): A TOTAL EVIDENCE ANALYSIS

Thèse présentée par Arnaud HENRARD en vue de l'obtention du grade de docteur en sciences

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GENERAL ABSTRACT

This PhD thesis mainly aims at the systematic revision of the spider family Zodariidae Thorell, 1881 on a global scale. While examining biological material for morphological character scoring, numerous specimens appeared to belong to unknown taxa to science. These undescribed zodariids showed characters that could be informative to understand the phylogenetic relationship among taxa. Subsequently, taxonomic description of several new zodariid taxa was undertaken in order to document these significant structures that had not been observed in spiders so far. It follows that, along with the description of the new genus *Palindroma* Jocqué & Henrard, 2015, a new synapomorphic feature was discovered (actually a small rounded tibial projection fitting into a metatarsal pouch), which strongly consolidated the monophyly and diagnosis of the family itself. Another remarkable feature, a double femoral gland on each leg, was found to characterize some typical representatives of the Zodariidae that are compulsory ant-eaters. As a result, two new genera, *Suffrica* Henrard & Jocqué, 2015 and *Suffascar* Henrard & Jocqué, 2017 were described and a preliminary, morphology-based, cladistic analysis of the 'femoral organ group' was conducted. Two different groups, the dual (DF) and the single femoral (SF) organ clades, were recognized, sharing a sister-group relation. However, the evolution of the femoral organ glands remains uncertain. Furthermore the old question about the validity of the status of the subfamily Storeninae, which had been fused into the Zodariinae, was placed back on the table.

Ultimately, I revised the phylogenetic relationships of the entire family using a combined approach based on morphological and molecular data. Among other specific questions to be solved, I intended to further investigate the proposed monophyly of the subfamilies established by Jocqué in 1991a: Cyriocteinae, Lachesaninae, Storenomorphinae, Cryptothelinae (ex Cydrelinae), Storeninae and Zodariinae. The present study represents the largest

taxonomic sample of Zodariidae analyzed to date. A character matrix was built, comprising 153 morphological characters spread over 11 structural groups. The molecular data included 5 genetic markers: 1 mitochondrial (COI) and 4 nuclear markers, including sequences of protein coding genes (Act5C, H3) and ribosomal genes (18S, 28S). In order to assess the phylogeny of the Zodariidae, different analyses were performed (based on morphological, genetic and combined datasets) using different statistical approaches (Maximum Likelihood, Bayesian inference and parsimony (for morphological data)).

The combined results highlighted 5 groups corresponding to 5 sub-families. As predicted, the Cyriocteinae appeared sister to all remaining Zodariidae in the morphological analysis. However, this finding could not be confirmed by the molecular analysis due to the lack of fresh biological material. The Lachesaninae, Cryptothelinae and the Zodariinae are redefined. The Storenomorphinae were found paraphyletic in the molecular and combined analyses and fall into Cryptothelinae. As a consequence, Storenomorphinae were fused with the Cryptothelinae. The Storeninae were re-established and redefined. *Procydrela procursor* Jocqué, 1999 could not be assigned to any subfamily and we may consider to place it in a group of its own.

Among the Zodariinae, the femoral organ clades (DF+SF) were strongly supported in the combined analysis. Surprisingly the molecular analyses only supported the SF clade. The femoral organ is a quite complex structure implying the development of a gland on an unusual location for a spider. It is therefore very unlikely that this character has developed twice. However, even based on the morphological and combined analysis, the evolution of the femoral organ and its complexity remain ambiguous and not fully resolved.

CHAPTER I

GENERAL INTRODUCTION

TAXONOMY AND BIODIVERSITY

Knowing how many species are on Earth and how many will disappear before discovering them are amongst the major challenges in biological science, while we are probably experiencing the fastest loss of biodiversity since the extinction of dinosaurs (Agnarsson and Kuntner 2007; Barnosky et al. 2011; Ceballos et al. 2015; Leasi et al. 2018). In the past 250 years of research, taxonomists have described and named about 1.8 to 1.9 million living species (Gaston and May 1992; Singh 2002; May and Harvey 2009). However, taxonomic knowledge is far from complete. Estimates made over the past 30 years on the total number of living species are still subject of debate and the upper limits range from 7 to 80 million or more (Erwin 1982; 1988; Stork 1988). Nevertheless, most authors agree for narrower approximation of about 2-12 million (May 1988; Stork, 1997; Gaston 1991; May and Harvey 2009; Mora et al. 2011; Costello et al. 2012; 2015a).

Whereas the most common and widespread species were discovered long times ago, most of the newly discovered species are predicted to be those having very small geographical ranges, being especially rare or living in remote areas (Pimm et al. 2014, Costello et al. 2015b; Lees and Pimm 2015). Unfortunately, those species are likely to be endangered. The environmental impact of human activities is observable throughout the world, provoking dramatic changes in biodiversity patterns of various habitats and ecosystems. Yet, species classified as “critically endangered” are not only naturally rare but also occur in places suffering of extreme habitat destruction and degradation, being restricted to remnants of once extensive habitats (Lees and Pimm 2015). In addition to the important habitat loss (Daily 1995), many endangered species are also losing substantial genetic variation as their populations collapse, leading to deleterious genetic effects and reduced viability (Laurance 2013).

We know that biodiversity is essential for ecosystem functioning and stability and, as a consequence, also vital for human survival and its economic well being (Singh 2002; Kim and Byrne 2006). Preserving biodiversity and its taxonomic component is thus securing human future. Nevertheless, since the last decades, many studies warn that we have entered into the 6th phase of mass extinctions (Pimm and Raven, 2000; Dirzo and Raven 2003; Thomas et al., 2004; Kim and Byrne 2006; Barnosky et al. 2011) with current rates of extinction thousands times higher than the background rate inferred from the fossil record (Singh 2002; May and Harvey 2009).

While species are disappearing at an ever-increasing rate, the field of taxonomy (species discovery and description) is facing a crisis: dwindling interest and lack of resources undermine the continuity of cataloguing biodiversity (Godfray 2002; Wilson, 2004; Wheeler, 2004; 2005; Korf 2005; Agnarsson and Kuntner 2007; Bacher 2012). Though, some authors seem having noticed a recent regain of taxonomic efforts (Costello et al. 2012; 2013; 2015a). However, taxonomy, together with ecology, are the fundamental sciences that generate the knowledge about biodiversity (Kim and Byrne 2006). Both are essential to acquire detailed information on species composition of specific areas, to understand how different species contribute to ecosystem services and ultimately to provide the information on how to sustainably conserve and manage biodiversity. Considering the threats on habitats and biodiversity, new knowledge on existing species and discovery of undescribed species and their subsequent study are urgently required (Costello et al. 2015b).

WHAT IS TAXONOMY ?

Taxonomy, or more broadly Systematics, is the scientific discipline that aims at describing, naming and classifying all organisms on earth, both living to extinct species. This work is essential for the fundamental understanding of biodiversity and its conservation.

Naming species is not only a first step in documenting knowledge about their biology or biogeography, it also provides an indispensable database for ecology and conservation science. Taxonomy is at the base of biodiversity science because it exceeds the discovery of new species (Costello et al. 2015a). Once a species is described, more detailed studies can deepen our knowledge on diversity at the level of populations, genetics or biochemistry. Knowing what species exist is a prerequisite for insight in how many and which species are threatened of extinction. Up to date taxonomy is also crucial to understand whether the species that are no longer reported have disappeared as a result of a nomenclatorial problem and are now referred to under a different name (Carlton et al. 1999). Indeed, whereas the total number of known species is currently estimated at nearly 2 million, with all the synonymies removed it may be 1.6 million or fewer (May and Harvey 2009).

Although taxonomy has its origins in ancient Greece (Godfray 2002), the starting point of its modern form dates back to when Linnaeus, in 1758 introduced the concept of binomial nomenclature, which is still in use since the 10th edition of the *Systema Naturae* (Linnaeus, 1758). Exceptionally however, arachnologists have rather considered the significant publication *Aranei Svecici* of Clerck (1757) as the reference for taxonomy of spiders (Bonnet 1944; 1947; Pleijel and Rouse 2003; Kuntner and Agnarsson 2006; Platnick and Raven 2013).

Binomial nomenclature, the Linnaean system, is based on types (type specimens for species and type species for genera) and assignment of ranks or categories (hierarchy from kingdom to species) (Dubois 2005). It is ruled by several International Codes of Nomenclature (*e.g.* for algae, fungi, and plants (Turland et al. 2018), for prokaryote (Parker et al. 2019), and for animals (ICZN 1999)). Recently, however, the classic system was criticized and has been regarded inappropriate for the naming of clades (Cantino and de Queiroz, 2004).

A recent alternative, a rankless approach called "phylogenetic taxonomy" (de Queiroz & Gauthier 1990; 1992; 1994) was proposed and is ruled by the International Code of Phylogenetic Nomenclature (called PhyloCode) (Cantino and de Queiroz, 2004). This new practice is actually debated but a compromise approach between the rules governed by Linnaean hierarchy and phylogenetic nomenclature seems possible (Kuntner 2005; 2006; Kuntner and Agnarsson 2006). Roughly, the directives for species names remain governed by the binomial rank-based Nomenclature codes, and, even if practical reasons argue for the additional retention of the classical ranks (family, order, class, kingdom, phylum), the PhyloCode would regulate the clade naming (based on monophyly) at all levels (Kuntner and Agnarsson 2006).

PHYLOGENETIC SYSTEMATICS

Among its plethora of derivative functions, taxonomy also lays the foundations for the phylogenetic tree of life: indeed, without taxonomy phylogeny is impoverished (Wilson 2004; Wheeler 2004; Korf 2005; Agnarsson and Kuntner 2007). Phylogeny can explain a wide range of biological patterns, one of its major advantages being the predictive possibilities implied in the structure of a tree (Coddington 2005; Wheeler 2005). Knowing one feature predicts many others: e.g. all spiders share some particular features because they inherited them from a common ancestor, even if, in the course of evolution, today's spiders have evolved to differ among themselves (Coddington 2005). The phylogenetic classification theory was first formalized by the German entomologist Willy Hennig (1966). Hennig called it 'phylogenetic systematics' but the name 'cladistics' has become the most popular (Ridley 1997). Once organisms are recognized and named, it is evident that they are classified. What and how named groups should be recognized and how they should be subdivided are the primary concerns of a theory of classification, i.e. systematics (Nelson and Platnick 1981).

Natural classifications are based on inferred phylogenetic relationships, which attempt to highlight that all representatives of a particular group share a common ancestor. Hennig (1966) had realized that if life has diversified over time, then there has to be a hierarchy of taxonomic characters that is an exact mirror of that history (Platnick 2016). Then, understanding that shared patterns inherited from common ancestry (synapomorphies) are the links connecting all species, he introduced the theory phylogenetic systematics as a means to improve the information content of classifications and names. This theory that works with homologous characters (Wiley et al. 1991; Ridley 1997), provides a general reference system for biology (Wheeler 2004). Hennig (1966) distinguished apomorphies (derived characters) from plesiomorphies (ancestral characters) and made phylogenetic constructs open to rigorous testing (Schuh 2000). It is only the presence of one or more synapomorphic character transformations (shared derived characters) that can delineate a group. There are other similarities that do not characterize a group in this way, and if a proposed group has no putatively synapomorphic character(s) that support it, then there is no evidence that the group is not simply artificial (Platnick 2016). The task of taxonomists is thus clear: finding the synapomorphies that allow us to construct a single hierarchy uniting all taxa.

Today, in the age of molecular systematics, the evolutionary relationships of most studied groups are mainly inferred from molecular sequences or even genome scale data. DNA is the inherited material and the use of nucleotide sequences for studying phylogeny offers a much larger number of potential characters for comparison. Despite an ever-increasing reliance on molecular sequence data for phylogeny reconstruction and evolutionary inference, morphological characters remain an important source of phylogenetic signals (Wiens 2004; Will & Robinoff 2004; Will et al. 2005; Schultz 2007) (both alone and in combination with molecular data). They remain essential for reconstructing and exploring evolutionary patterns.

TARGETING MEGA-DIVERSE GROUPS

As mentioned earlier, while we are currently undergoing a rapid and tremendous loss of biodiversity, our earth's taxonomic knowledge is still in its infancy. Conservation priorities imply the identification of "biodiversity hotspots" where exceptional concentrations of endemic vertebrate and plant species are correlated with exceptional loss of habitat (Myers et al. 2000; Mittermeier et al. 2005). However, it is the invertebrates, especially the arthropods, which represent the largest part of the biodiversity on earth (Meier and Dikow 2004; Tixier and Kreiter 2008). They are very diverse groups that have much smaller and fine-grained geographic ranges than do most vertebrates or plants. Such mega-diverse and micro-distributed groups are expected to yield detailed information about the distribution pattern of biodiversity on the planet (Nelson and Platnick 1981; Platnick 1999). What is needed is detailed knowledge on the distribution and interrelationships of a few taxonomic groups, each with numerous allopatric species. This knowledge would allow localizing narrow areas of high diversity or endemism and could be used to choose, for conservation purposes, the set of areas that can jointly maximize the phylogenetic diversity we may still be able to save (Vazquez and Gittleman 1998; Platnick 2006).

Among the plethora of arthropod groups, several characteristics associated with arachnids make them excellent biodiversity indicators. Most arachnid taxa have small distribution ranges, and species found in an area are likely to be resident in that area (Griffin 1998). Among them, spiders are specially indicated for several reasons: they belong to such mega-diverse groups with micro-distributed species (Coddington and Levi 1991; Colwell and Coddington 1994; Griswold et al. 1999) and these small organisms can teach us a lot about the distribution of biodiversity on the planet. Spiders comprise over 2% of all the described species on the planet (Platnick 2006) and with more than 48.000 species (WSC 2018), spiders definitely represent the most

varied group of venomous predators (Pekár et al. 2018a). They are the most common terrestrial predators and, because of their abundance, they are the most important hunters of insects, making them a primordial ecosystem component. Some studies even mention spiders as potential predators to control insects in orchards and agricultural crops (Rajeswaran et al. 2005; Memah et al. 2014; Lefebvre et al. 2017). Spiders have also already been proposed as indicators of habitat quality or to establish conservation priorities (e.g. Maelfait and Baert 1988; Jocqué et al. 2005; Ysnel et al. 2008). Besides that, spiders are easy to collect and fairly easy to be identified (for specialists) (Marusik and Koponen 2000). Indeed, they show external genitalia which are the keystones for their identification and which do not need complicated methods of preparation to be examined. Furthermore, there is the great advantage for having a fully completed database of spider taxa: the scattered taxonomic knowledge of spiders has been completely catalogued in an electronically available form: The World Spider Catalog (online at http://wsc.nmbe.ch). All these characteristics rank them among the most accessible groups for the purpose of rapid biodiversity estimations and assessing local biodiversity value (Skerl and Gillespie 1999).

In this context, however, it is clear that the results obtained by phylogeny are necessary and meaningful only if they are part of a reliable taxonomic set. Indeed, a taxonomic framework in which the entities (species or taxa) are clearly defined is fundamental. In order to establish such a taxonomic framework, it is essential to carry out a systematic and phylogenetic revision of the biological material studied. Among Spiders, the Zodariidae exhibit such a combination of features, being a diversified family including micro-distributed species. Furthermore, it was the first spider family studied on a global scale and in a cladistic context (Jocqué 1991a). This background makes it therefore the ideal group for the application of a detailed phylogeny based on molecular tools, in combination with morphological data.

With this thesis, as it is clear that the use of phylogenetic information in taxonomy is a useful and powerful tool, mainly in the field of systematics, the intention is to use a combined and multigene phylogenetic approach to revise, on a global scale, a diversified spider family, the Zodariidae.

THE SPIDER FAMILY ZODARIIDAE

The spiders (Arachnida; Araneae) belong to a strongly diversified arthropod group, in which a wide variety of trophic strategies have evolved. Although with nearly 50.000 species described to date, experts agree that even half of extent spider species have not yet being discovered (Agnarsson et al. 2013; Kuntner and Agnarsson 2018). Distributed in 117 families, spiders are by far the most diversified group of venomous predators (Pekár et al. 2018a). Among them, the Zodariidae Thorell, 1881 (Fig. 1), commonly named "burrowing spiders" or "ant-eating spiders", represent a medium sized family of spiders. With 1143 zodariid species disseminated in 85 genera, they rank 12th of the most diverse spider families according to the World Spider Catalog (WSC 2018). Zodariids are mainly distributed in tropical and subtropical regions whereas few genera have reached the temperate region (Jocqué and Dippenaar-Schoeman 2007).

The zodariids are wandering, mainly nocturnal, ground-dwelling spiders. They apparently have limited dispersal capacities as they have never been observed to perform ballooning nor in air samples (Ramírez 1995; Pekár 2002), a dispersal behavior used by numerous spider taxa (Bell et al. 2005). Most species occur in arid or semiarid areas, living in the sand, among rocks or in vegetation. Some genera appear to be strongly tied to rainforest, living mainly in the leaf litter (e.g. *Mallinella* Strand, 1906, *Dusmadiores* Jocqué, 1987) but also in higher strata of the vegetation such as bushes and trees (e.g. *Asceua* Thorell, 1887; *Storenomorpha* Simon, 1884). The zodariids that have the ability to burrow are often named "burrowing spiders".

Figure 1. Zodariidae diversity. A. *Cyrioctea marken* Platnick & Jocqué, 1992, male (RMCA_ARA_245374), Limpopo, South Africa © Arnaud Henrard. B. *Selamia reticulata* (Simon, 1870), female (specimen DNA Z075), Aude, France © Arnaud Henrard. C. *Cryptothele* sp., Singapore © Nicky Bay. D. *Cydrela schoemanae* Jocqué, 1991, male, Gauteng, South Africa © Peter Webb. E. *Chariobas sp.*, male, KwaZulu-Natal, South Africa © Peter Webb. F. *Cybaeodamus meridionalis* Lise, Ott & Rodrigues, 2009, female, Santa Fe, USA © Martín Ramírez. G. *Habronestes hunti* Baehr, 2003, male, Queensland, Australia © Robert Whyte. H. *Mallinella* sp. Strand, 1906, female, Nimba Mountains, Guinea © Arnaud Henrard. I. *Zodarion italicum* (Canestrini, 1868), male with ant as prey, Ille-et-Vilaine, France © Arnaud Henrard.

However, some representatives do not burrow but construct retreats with soil particles or plant debris, most often located under stones or hidden in the litter. The spiders of this group are often called “ant-eating spiders” as they are essentially, if not entirely compulsory ant or termite eaters (Jocqué 1988b; Jocqué and Dippenaar-Schoeman 1992; Pekár 2004, Pekár et al. 2005; Cárdenas et al. 2014; Komatsu 2016).

In Zodariidae, myrmecophagy is considered as a derived trophic strategy but euryphagy can still be found in more plesiomorphic taxa (Pekár et al. 2012a; 2013; Pekár and Lubin 2009; Pekár and Toft 2015).

THE ZODARIIDAE SYSTEMATICS

The Zodariidae are among the most diversified spider families, having an impressive size range and an enormous variation of shapes (Jocqué 1991a; Jocqué et al. 2013; Jocqué and Dippenaar-Schoeman 2007; Russell-Smith and Jocqué 2015). The family was already fairly well defined by Simon (1870) and the Zodariidae were then characterized by a combination of morphological characters including the absence of a serrula on the endites, the stronger anterior lateral spinnerets (ALS) (compared to the others) and the laterally inserted teeth on the tarsal claws (Jocqué 1991a; Jocqué and Dippenaar-Schoeman 2007). However, these characters, taken independently, are also present in various taxa belonging to other families (Ramírez et al. 2014). In the revision at generic level by Jocqué (1991a), the definition was corroborated in a cladistic analysis and six subfamilies were defined (Fig. 2): Cyriocteinae, Lachesaninae, Storenomorphinae, 'Cydrelinae' (= Cryptothelinae), Storeninae and Zodariinae. However, the Storeninae appeared paraphyletic and, due to lack of autapomorphies, this subfamily was later fused into the Zodariinae (see Jocqué 1992)

The status of some taxa such as *Cryptothele* (Jocqué and Dippenaar-Schoeman 2007) or *Cyrioctea* remained questionable. In the latter, the teeth on the paired tarsal claws are not inserted laterally (as in derived zodariids) but medially. *Cyrioctea* was therefore proposed to be the sister group of all remaining zodariid taxa (Platnick 1986; Platnick and Griffin 1988) and was used as the outgroup in the cladistic analysis of Jocqué (1991a) (see Fig. 2), thus excluding the possibility to truly test its relationships to other taxa.

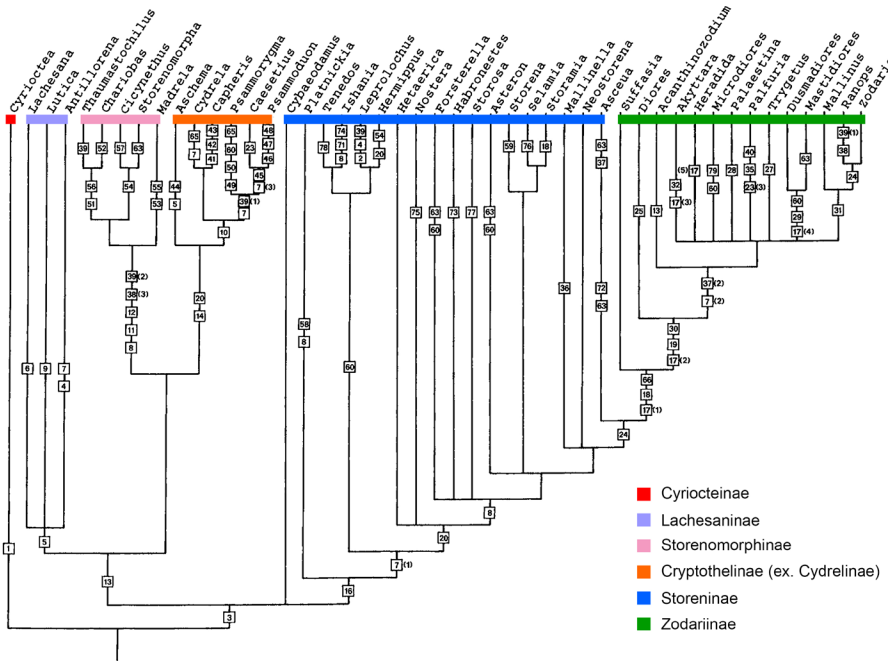

Figure 2. Cladogram of zodariid genera (adapted from Jocqué 1991a, fig. 41). The consensus tree was obtained from 140 equally parsimonious trees and is based on 79 morphological characters. Colors represent sub-families as defined in Jocqué (1991a).

Until recently, the phylogenetic placement of the Zodariidae itself was not totally clear (e.g. Coddington and Levi 1991; Coddington et al. 2004; Coddington 2005; Dippenaar-Schoeman and Jocqué 1997; Jocqué and Dippenaar-Schoeman 2007).

The family was sometimes associated with Homalonychidae (Simon 1893; Roth 1984; Wunderlich 2004), considered part of the Amaurobioidea (Jocqué and Dippenaar-Schoeman 2007) or placed in a polytomy with Dionycha and Amaurobioidea (Coddington and Levi 1991; Coddington et al. 2004; Coddington 2005; Ramírez 2014).

THESIS PURPOSES

Since the cladistic review of Jocqué (1991a), 37 genera have been added to the diversity of the Zodariidae (WSC 2018). However, many

taxa still remain to be described. The description of some unknown zodariid taxa prior to the publication of phylogenies is undertaken in order to document some remarkable combinations of features that have not been observed in spiders so far. Among these characters, those linked to the femoral organ are of particular interest. A preliminary, morphology-based cladistic analysis of the femoral organ group is initiated in order to unravel the evolution of the femoral glands.

The cladistic approach used in the study of Jocqué (1991a) was fairly rudimentary and contains some flaws (see Dankittipakul et al. 2012) reflecting the methodology in the early days of cladistics. For instance, in his analysis, the outgroup was *Cyrioctea* (see Fig. 2), which should have been part of the ingroup. To date, mainly internal phylogenetic inferences were focused on some taxa or groups of taxa (see Dankittipakul et al. 2012 for an exhaustive list) and all have been restricted to morphological characters. This work intends to further investigate the proposed monophyly of the subfamilies established by Jocqué in 1991a: Cyriocteinae, Lachesaninae, Storenomorphinae, Cryptothelinae (ex Cydrelinae), Storeninae and Zodariinae.

The present study represents the largest taxonomic sample of Zodariidae analyzed to date and firstly aims to infer the phylogeny of the entire family on a global scale using a combined approach of both molecular and morphological data. A related objective of this latter goal, is to re-evaluate the monophyly of the different subfamilies established by Jocqué (1991a; 1992) and to test the placement of peculiar taxa such as *Cyrioctea*, *Cryptothele* and other "problematic" taxa in the Zodariidae. The study of the relationships among its genera will provide the opportunity to understand and interpret the evolution of morphological and behavioral traits, such as the predation on ants and the evolution of the femoral glands.

CHAPTER II

PALINDROMA GEN. NOV., WITH NOVEL ZODARIID SYNAPOMORPHY

The Zodariidae family was already fairly well defined by Simon in 1870 and, in the revision at generic level by Jocqué in 1991a, the definition was corroborated by a cladistic analysis. However, the status of some peculiar taxa still remained questionable (e.g. *Cryptothele*, *Cyrioctea*). Until recently, the phylogenetic placement of the Zodariidae itself was not totally clear and the Zodariidae were characterized by a combination of morphological characters (Jocqué 1991a; Jocqué and Dippenaar-Schoeman 2007). However, these characters, taken independently, are also present in various taxa belonging to other families (Ramírez et al. 2014).

During the examination of materials used for morphological character scoring, numerous samples were discovered to belong to taxa unknown to science. Along with the description of a new taxon in the Cryptothelinae in 2015, a so far unnoticed morphological character was found and appeared to be also present in other zodariid taxa. The discovery of such an informative synapomorphic feature, actually a small rounded tibial projection fitting in a metatarsal pouch, strongly consolidated the diagnosis of the family and removed any doubt on the inclusion of plesiomorphic taxa such as *Cyrioctea*.

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Contribution of the second author: *Arnaud Henrard contributed in the description of the new genus and species, in taking photos and SEM views, in preparing the illustration plates, in screening and documenting the peculiar synapomorphic character in a large series of Zodariidae and non Zodariidae and in reviewing the main text.*

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Research article

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The new spider genus *Palindroma*, featuring a novel synapomorphy for the Zodariidae (Araneae)

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Abstract. The new genus *Palindroma* gen. nov. is described in the Cryptothelinae, Zodariidae. Apart from the type species, *P. morogorom* gen. et sp. nov. (♂♀), the genus contains *P. aleykyela* gen. et sp. nov. (♂), *P. avonova* gen. et sp. nov. (♂♀), *P. sinis* gen. et sp. nov. (♂) and the somewhat aberrant species *P. obmoimiombo* gen. et sp. nov. (♂). The four typical representatives of the genus are characterized by the profile of the carapace with a slight dip, the absence of precoxal sclerites and the characters of the male palp with enlarged tibia, large subtegulum and tegular retrolateral knob. The genus occurs in miombo-woodland and coastal forest in East and Central Africa and this peculiar distribution is discussed. A key to the males of the *Palindroma* species is provided. Specimens of *Palindroma* have a particularly well-developed tibial process fitting in a shallow metatarsal pouch on all legs in both sexes. Although less conspicuous in some derived taxa, the feature appears to be present in all representatives of the Zodariidae, but not in possible sister-group taxa and is thus an autapomorphy of the family.

Keywords. East Africa, Central Africa, Cryptothelinae, miombo, tibial process.

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Introduction

Probably the most confusing area in the systematics of the Zodariidae is the subfamily Cryptothelinae, which has been mentioned under the name Cydrelinae until the genus *Cryptothele* L. Koch, 1872 was eventually incorporated into it (Jocqué & Dippenaar-Schoeman 2007; Ramirez *et al.* 2014). Many species had been misplaced, mainly due to the poor definition of the genera before the revision of Jocqué (1991). As a consequence, several new genera were created to accommodate the many species that had either been misplaced or that remained to be described. The Cryptothelinae has its main distribution in southern Africa and appears to be far from completely inventoried. Some large genera (*Cydrela* Thorell, 1870; *Psammorygma* Jocqué, 1991) remain to be revised and many species have not yet been described, partly because they do not fit in one of the current genera. In the present article a new genus is created to accommodate five new species.

The family Zodariidae can be considered as well defined. However, it remains one of the most diversified spider families: it not only has a huge size range (see Jocqué *et al.* 2013; Russell-Smith & Jocqué 2015) but the variation of the habitus and of morphological characters is so vast that a superficial scan of a specimen does not always easily reveal its generic or even (sub-)familial identity. Mainly for the taxa at the base of the clade (see Jocqué 1991), there may be some doubt about their inclusion in the family. Some of them (e.g., *Cyrioctea* Simon, 1889) lack the typical lateral claw teeth and are incorporated in the Zodariidae solely on the base of the absence of the serrula on the endites. The new synapomorphy, a prolateral tibial process on all legs in both sexes discovered during the description of the new genus, is therefore most welcome since it corroborates the inclusion of basal taxa.

Material and methods

Specimens were observed, drawn and measured with a WILD M10 stereo microscope. Details of the female genitalia and male palps were observed with a Zeiss Stemi 2000 stereo microscope. Measurements and photographs of the habitus, details of mouthparts, detached male palps and female genitalia were taken with a Leica MZ16 using the LAS automontage software (ver. 3.8). The female genitalia were dissected and digested with pancreatin, and then immersed in 75% ethanol.

For SEM photos, specimens were dried in hexamethyldisilazane (36 h), gold coated and examined and photographed with a JEOL 6480 LV scanning electron microscope. Types are deposited in the Royal Museum for Central Africa, Tervuren, Belgium (MRAC) and the Zoological Museum, Natural History Museum of Denmark, University of Copenhagen (ZMUC).

All measurements are in mm. All palp illustrations are from right palps. Leg spination formulas follow Jocqué (2013).

Abbreviations

ALE	=	anterior lateral eyes
AME	=	anterior median eyes
ALS	=	anterior spinnerets
d	=	dorsal
disp	=	spines dispersed and not in clear rows
dw	=	distal whorl of spines
F	=	femur
MRAC	=	Musée Royal de l'Afrique Centrale (Tervuren, Belgium)
Mt	=	metatarsus
P	=	patella
pl	=	prolateral
PLE	=	posterior lateral eyes
PLS	=	posterior lateral spinnerets
PME	=	posterior median eyes
PMS	=	posterior median spinnerets
rl	=	retrolateral
RTA	=	retrolateral tibial apophysis
t	=	tarsus
T	=	tibia
v	=	ventral
ZMUC	=	Zoological Museum, Natural History Museum of Denmark, University of Copenhagen

Taxonomy

Class Arachnida Cuvier, 1812
Order Araneae Clerck, 1757
Family Zodariidae Thorell, 1881
Subfamily Cryptothelinae Simon, 1892

Palindroma gen. nov.
urn:lsid:zoobank.org:act:2FF14DA8-1CEB-4F1A-941F-1DE1B368257D

Type species

Palindroma morogorom sp. nov.

Diagnosis

Representatives of *Palindroma* gen. nov. are typical sturdy Cryptothelinae with ALE in front of AME and slightly recurved to straight posterior eye row; sternum shield shaped with straight anterior margin and without precoxal sclerites; posterior legs with numerous short spines in combination with longer ventral spines; teguments of carapace, legs and abdomen often provided with patches of white or silvery setae. Male palp with large patella, large subtegulum and tegulum provided with retrolateral knob; median apophysis absent.

Palindroma gen. nov. is easily separated from *Capheris* Simon, 1893 and *Systenoplacis* Simon, 1907 by the absence of anterior concavities of the sternum. It deviates from *Caesetius* Simon, 1893, *Psammorygma* and *Rotundrela* Jocqué, 1999 by the absence of precoxal sclerites, from *Aschema* Jocqué, 1991 by the unmodified posterior legs and from *Psammoduon* Jocqué, 1991 by the absence of fans of supple spines on the legs; in *Cydrela* the sternum is slightly indented in front, the cephalic area in the carapace profile much higher and the posterior eye row more strongly recurved.

Etymology

The genus name is derived from the English term 'palindrome' originating from the Greek 'παλινδρομος', that refers to words or sentences that are identical whether they are read from front to back or the other way round. All species names of the new species described here are palindromes. The gender of the species name is feminine.

Description

Medium size spiders (7.5–10 mm) with reticulated to roughly granulate teguments. Carapace longer than wide (L/W < 1.43–1.71), slightly protruding anteriorly, with silvery hairs in male, almost hairless in females apart from a few longer hairs on clypeus; widest at level of coxae II–III, narrowed to about 0.48–0.62 times maximum width in males and 0.62–0.71 times maximum width in females (cephalic width measured on posterior tangent of PME). Cervical grooves poorly indicated. Profile flat or domed, highest at level of first coxae and with slight dip at level of fovea.

Colour: carapace medium to dark brown; chelicerae, legs, mouthparts and sternum medium to orange brown; abdomen dorsum grey with one to seven pale spots and four reddish apodemes, sides and venter white to pale grey; in males sclerotized in front of epigastric fold.

Eyes in three rows: ALE in front of AME and further apart, posterior row straight or slightly recurved and eyes far apart. All eyes subequal, AME dark, other eyes pale. Clypeus straight, slightly slanting back, height 2.5 to 4 times diameter of ALE, sometimes with some long dispersed setae.

Chilum double, about or slightly more than twice as wide as high, lateral margin poorly defined; without setae. Chelicerae slightly conical, inner margin almost straight, with many evenly dispersed setae; with distomesal membranous lamina (Fig. 1A–B); fangs shorter than wide at base. Labium inverted U-shaped, with slightly narrowed base. Endites roughly triangular, converging, with basolateral extension accommodating palpal coxae. Sternum shield-shaped, as wide as long, without triangular extensions or precoxal sclerites; anterior margin straight, lateral margins slightly sinuous.

Legs: robust. Formula 4123 or 4132. Spination reduced on legs I and II, well developed on III and IV. Most spines short and thick except dorsal ones on F and ventral ones on T and Mt. Patella III and IV with retrolateral boss at base of short spine. Anterior tarsi fusiform in male, usually longer than metatarsi, unmodified in female. One dorsal hinged hair on tibiae and metatarsi I and II (Fig. 1D). Trochanters with anterior concavity. Prolateral tibial process strongly developed on all legs in both sexes (see Fig. 17A–E). Three tarsal caws, paired ones with numerous teeth (Fig. 1C).

Female palp with numerous prolateral spines and some retrolateral ones (Fig. 1E); palpal claw with some small teeth at base (Fig. 1F); turned inward over less than 45°; without distal patch of chemosensitive setae.

Abdomen oval, with ventral row of small sclerotized apodemes; tracheal spiracle fairly small, somewhat advanced and provided with small rectangular scutellum. Both exes with six spinnerets. ALS large, conical, biarticulate. PLS and PMS provided with 1 and 3 cylindrical gland spigots, respectively. Colulus represented by haired field.

Male palp: complexity of palps very variable; patella larger than tibia (Fig. 2A), sometimes modified; RTA sometimes very small, in other species well developed. Cymbium with prolateral spines; without distal claw; sometimes with basal swelling(s); subtegulum strongly developed, sclerotized and visible in unexpanded palp; tegulum with retrolateral boss (Fig. 2B), variable in shape; embolus short, flat, distal part with flange.

Epigyne with central longitudinal depression. Spermathecae large, far apart; copulatory ducts with thick walls (Fig. 2C–F).

Note

The species *Palindroma obmoimiombo* gen. et sp. nov. is only tentatively and probably temporarily incorporated in the genus. It lacks several of the specific generic characters: the indented profile of the carapace, the membranous lamina of the chelicerae, the enlarged male palpal patella. On the other hand, it has a field with spinules on the flat mesal surface of the chelicerae. The latter character approaches conditions in *Caesetius* but that genus has a high domed carapace, precoxal sclerites and a much more strongly recurved posterior eye row. The species apparently belongs to an as yet undescribed genus but with only one species and in the absence of females we have refrained from creating a new genus for it.

Distribution

Palindroma is found in forest and miombo regions of central and eastern Africa in the Democratic Republic of the Congo, Malawi and Tanzania.

Key to males

1. Chelicerae almost rectangular as viewed in front, with distomesal extension well developed, without mesal field of spinules; carapace domed, with slight dip at level of fovea; palp with swollen patella, tibia with one RTA or RTA poorly developed ……2

– Chelicerae conical, with distomesal extension, inconspicuous, with mesal field of spinules; carapace profile flat, without dip; palp with unmodified patella, with two RTA ……***P. obmoimiombo*** sp. nov.

2. Carapace profile with slight dip at level of fovea; anterior tarsi with same length as metatarsi or longer; palp with conspicuous RTA ……3
– Carapace profile with marked dip at level of fovea; anterior tarsi shorter than metatarsi; palp with inconspicuous RTA ……***P. sinis*** sp. nov.

3. Anterior tarsi clearly longer than metatarsi; tegulum with well-developed basal or retrolateral extension ……4
- Anterior tarsi only slightly longer than metatarsi; tegulum with longitudinal ventral ridge ending medially in poorly developed knob ……***P. avonova*** sp. nov.

4. RTA thin, long and strongly tapered apically; tegulum sub-apically with retrolateral knob …… ……***P. morogorom*** sp. nov.
- RTA broad, short, with strongly sclerotized rounded extremity; tegulum basally with well-developed conical extension ……***P. aleykyela*** sp. nov.

Palindroma morogorom gen. et sp. nov.
urn:lsid:zoobank.org:act:20ACA48F-42F0-403C-A81A-21425B87484C
Figs 1A–F, 2A–D, 3A–G, 4A–D, 5A–C, 16, 17A–E

Diagnosis

The male of *P. morogorom* gen. et sp. nov. can be recognized by the long, strongly tapered RTA. The female has a characteristic epigyne with central depression showing two dark areas, flanked by a kidney-shaped area on either side and the inverted funnel-shaped pattern in front.

Etymology

The species name is an arbitrary combination of letters forming a noun in apposition and containing 'morogoro', the region where the types were found.

Material examined

Holotype

TANZANIA: ♂, Uzungwa Mts, Morogoro Region, Mwanihana Forest, 7°44'29.2" S, 36°53'17.7" E, 1800–1850 m, 25–29 Sep.1984, montane rain forest, pitfall trap, N. Scharff (ZMUC).

Paratypes

TANZANIA: 2 ♂♂, 1 ♀, together with holotype; 4 ♂♂, as previous; 1 ♂, as previous; 1 ♂, as previous; 4 ♂♂, as previous; 5 ♂♂, as previous (2 ♂♂ in MRAC 244094); 1 ♀, 28–29 Sep. 1984, further as previous; 1 ♂, 7°44'41.5" S, 36°53'12.9" E, 1650 m, further as previous; 1 ♂, as previous; 4 ♂♂, as previous; 1 ♂, 1650 m, 25–29 Sep. 1984, further as previous.

Other material

TANZANIA: 3 ♂♂, Uzungwa Mts, Iringa Region, Mufundi-Kigogo Forest Reserve, 8°40'00.5" S, 35°12'35.2" E, 1900 m, 7–15 Oct. 1984, montane rain forest, pitfall trap, N. Scharff (ZMUC); 2 ♂♂, as previous; 3 ♂♂, as previous; 1 ♀, 1700 m, 5–10 Oct. 1984, further as previous; 1 ♂, as previous; 1 ♂, 8°40'53.5" S, 35°14'59.1" E, 1700 m, 8–10 Oct. 1984, further as previous; 1 ♀, Uzungwa Mts, Iringa Region, Uzungwa Scarp Forest above Chita village, 8°40'53.5" S, 35°12'35.2" E, 750 m, 23 Oct.–14 Nov. 1984, lowland rain forest, N. Scharff (ZMUC); 1 ♂, 1600–1650 m, 8–13 Nov. 1984, montane rain forest, further as previous; 1 ♂, 1 ♀, Iringa district, Uzungwa scarp Forest Reserve, 11 km E of

Masisiwe village, Kihanga stream, 1800 m, 8°22'05.7" S, 35°58'41.6" E, 17–27 May 1997, ZMUC; 1 ♀, Uluguru Mts, Bunduki, Moy Mgeta, 7°20' S, 37°38' E, 30 Apr.–2 May 1957, P. Basilewsky & N. Leleup (MRAC 111892).

Note

Georeferences of the collections made in 1984 are approximations.

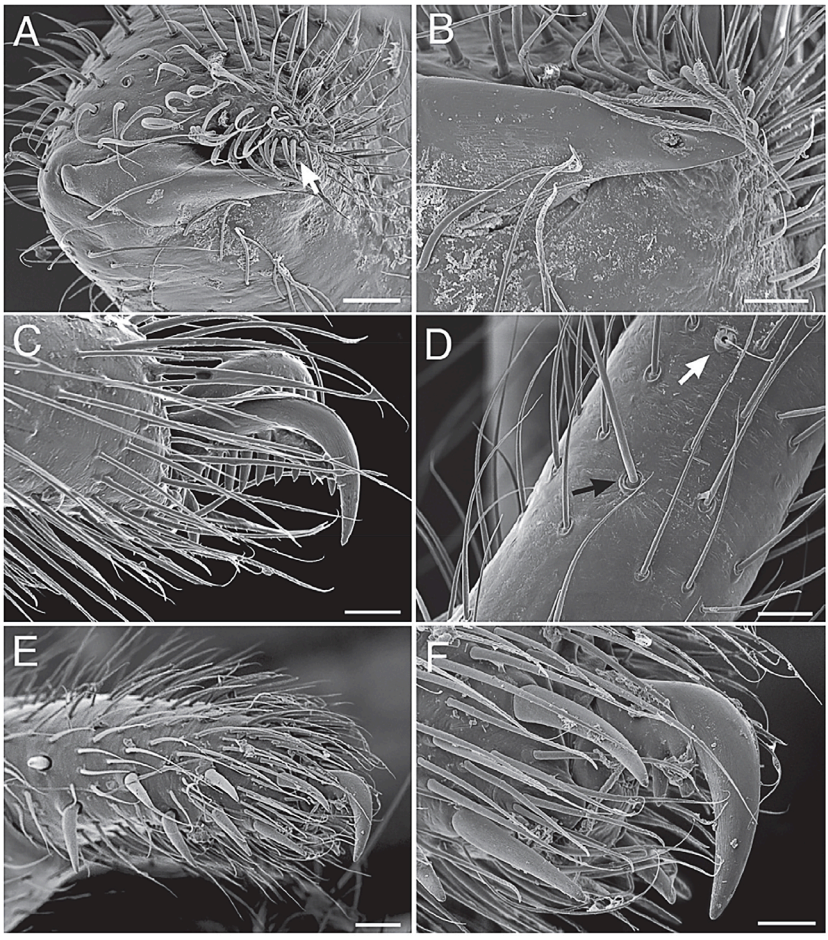

Fig. 1. *Palindroma morogorom* gen. et sp. nov. Scanning electron miocrographs. A–D. ♂ from Kigogo Reserve. E–F. Paratype ♀. **A**. Right chelicera, ventral view, arrow shows membranous lamina. **B**. As previous, detail. **C**. Leg I, tarsal claws, lateral view. **D**. Tibia I, hinged hair (black arrow), trichobothrium (white arrow). **E**. ♀ right palp, lateral view. **F**. Detail of previous. Scale bars: A, E–F = 100 mm, B–D = 50 mm.

Description

Male (holotype)
Total length 8.02; carapace 4.05 long, 2.77 wide, narrowed to 1.35 in eye region.

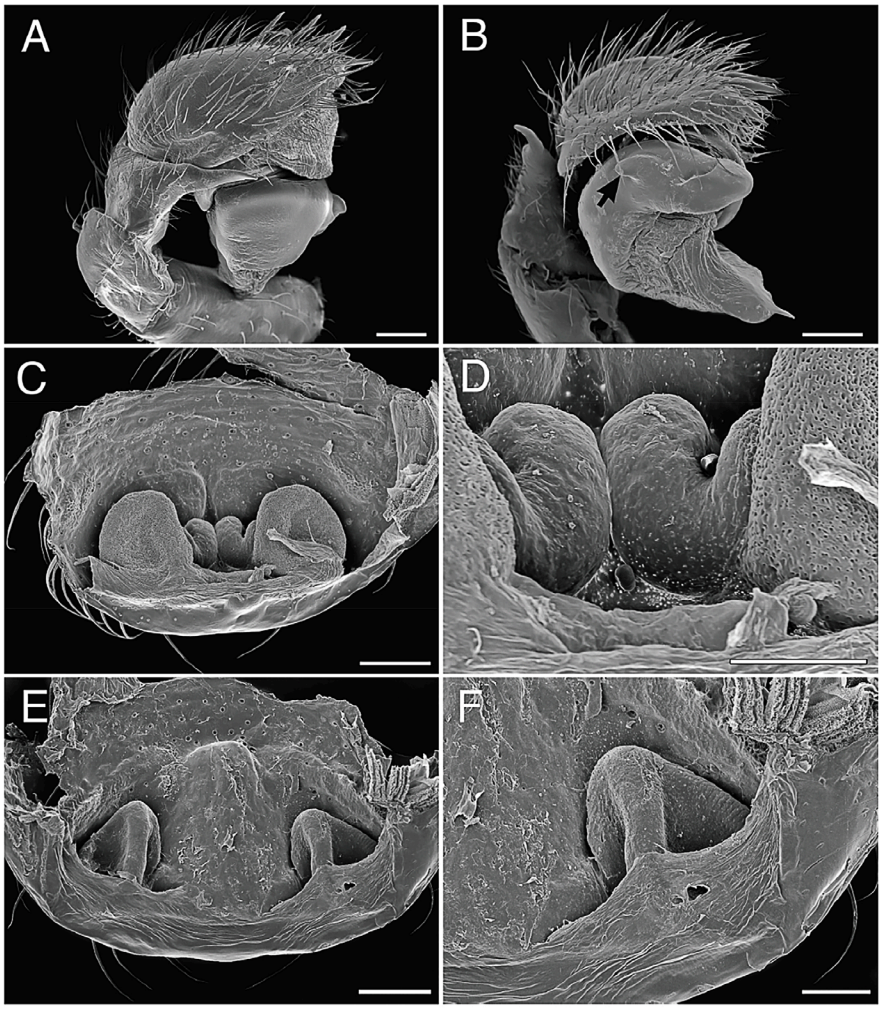

Fig. 2. — A–D. *Palindroma morogorom* gen. et sp. nov. Scanning electron miocrographs. A–B. ♂ from Kigogo Reserve. C-D. ♀ from Uzungwa Scarp Forest Reserve, paratype. A. ♂ palp, expanded, retrolateral view. B. Idem, anterolateral view. Arrow shows tegular retrolateral boss. C. Epigyne, digested, dorsal view. D. Idem, detail. — **E–F**. *Palindroma avonova* gen. et sp. nov., paratype, ♀. E. Epigyne, digested, dorsal view F. Idem, detail. Scale bars: A–C, E = 200 mm, D, F = 100 mm.

Colour: carapace and chelicerae medium brown without silvery setae (Fig. 3A, C–D); legs and sternum brownish orange (Fig. 3B); abdomen dorsum grey with pair of adjacent pale spots in front, a pair of pale spots in the middle followed by white bar and spot in front of spinnerets; four reddish apodemes in frontal half clearly delimited and two above the pedicel (Fig. 3A); sides grey with well delimited frontal apodemes; venter grey with lateral rows of apodemes and two rows of small apodemes behind well developed brownish epiandrum. Tracheal spiracle with small rectangular scutum followed by white membranous area in front of yellowish brown spinnerets.

Carapace granulated, cervical grooves slightly smoother (Fig. 3A). Clypeus with dispersed setae.

Eyes: AME: 0.12; ALE: 0.12; ALE-ALE: 0.21; AME-ALE: 0.16; PME: 0.12; PLE: 0.15; PME-PME: 0.13; PME-PLE: 0.31. Clypeus 0.54 or 4.5 times width of ALE.

Chilum double, each sclerite 0.10 high, 0.33 wide; no setae. Sternum shield-shaped, 1.42 long, 1.35 wide.

Legs: anterior tarsi longer than metatarsi.

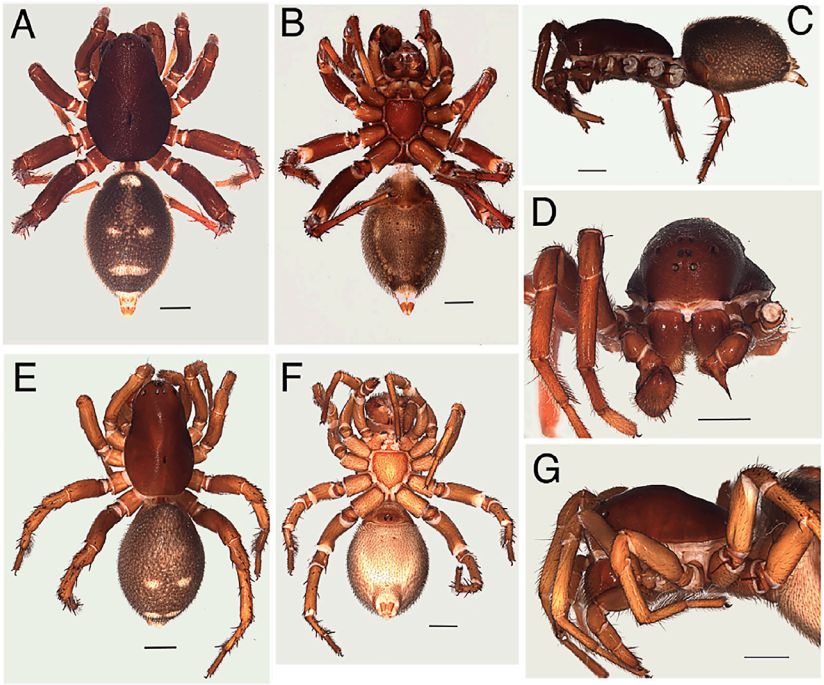

Fig. 3. *Palindroma morogorom* gen. et sp. nov. A–D. Paratype, ♂. E–G. Paratype, ♀. **A**. ♂, habitus, dorsal view. **B**. Idem, ventral view. **C**. Idem, lateral view. **D**. Idem, frontal view. **E**. ♀, habitus, dorsal view. **F**. Idem, ventral view. **G**. Idem, lateral view. Scale bars = 1 mm.

Spination

	F	P	T	Mt
I	d3	-	pl1	dw3
II	d3	-	pl1	dw2
III	d3	pl3d2rl1	pl2d45rl1v3	d1dw5
IV	d1	pl3d3rl1	pl2d5rl21v2	5dispdw5

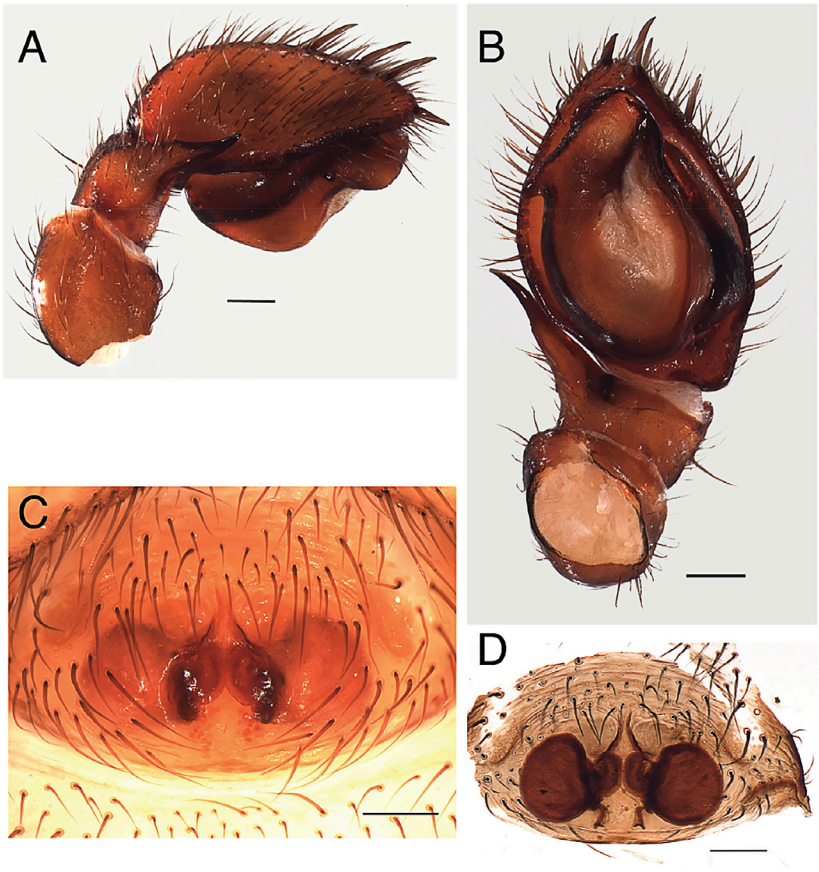

Fig. 4. *Palindroma morogorom* gen. et sp. nov. A–B. Paratype, ♂. C–D. Paratype, ♀. **A**. ♂, palp, retrolateral view. **B**. Idem, ventral view. **C**. ♀, epigyne, ventral view. **D**. Idem, cleared in methylsalicylate, dorsal view. Scale bars = 0.2 mm.

Leg measurements

	F	P	T	Mt	t	Total
I	2.10	0.91	1.61	1.33	1.40	7.35
II	1.82	0.91	1.26	1.19	0.98	6.16
III	1.89	1.05	1.26	1.26	0.91	6.37
IV	2.24	1.05	1.89	2.17	1.26	8.61

Male palp (Figs 2A–B, 4A–B, 5A–B): RTA with broad base strongly tapered to sharp extremity turned upward and outward; cymbium with several spines in distal half; subtegulum strongly sclerotized; tegulum with retrolateral knob; embolus originating on prolateral distal part of tegulum, broad at base, strongly tapered to sinuous sharp tip.

Female (paratype collected with holotype)
Total length 9.30; carapace 4.12 long, 2.41 wide, narrowed to 1.70 in eye region.

Colour: carapace chestnut brown with few silvery setae (Fig. 3E–G); chelicerae medium brown, sternum and legs orange brown; abdomen as in male but apodemes less well marked.

Carapace smooth. Clypeus with dispersed setae.

Eyes: AME: 0.13; ALE: 0.13; ALE-ALE: 0.31; AME-ALE: 0.23; PME: 0.15; PLE: 0.18; PME-PME: 0.14; PME-PLE: 0.38. Clypeus 0.59 or 4.5 times width of ALE.

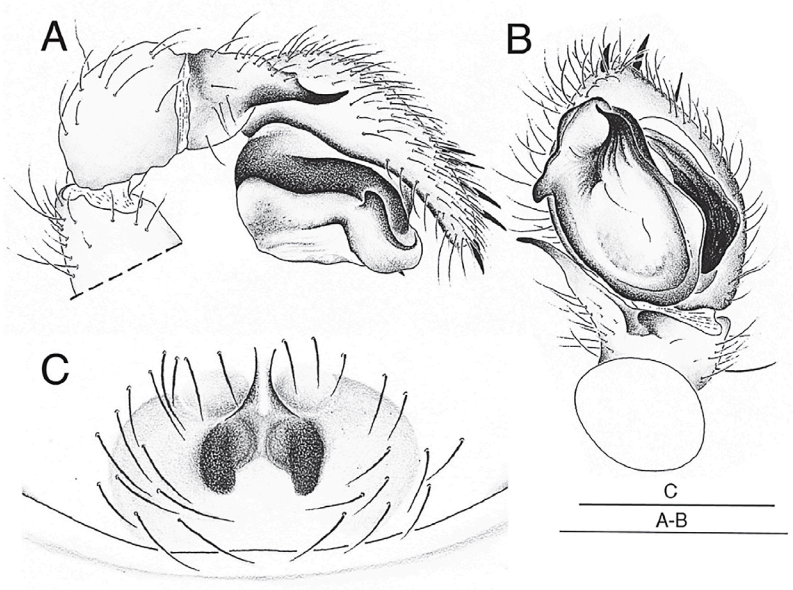

Fig. 5. *Palindroma morogorom* gen. et sp. nov. A–B. Holotype, ♂. C. Paratype, ♀. **A**. ♂, palp, retrolateral view. **B**. Idem, ventral view. **C**. ♀, epigyne, ventral view. Scale bars: A–B = 1mm, C = 0.5 mm.

Chilum double, each sclerite 0.10 high, 0.33 wide; no setae. Sternum shield-shaped, 1.42 long, 1.42 wide.

Legs: Anterior tarsi not modified, shorter than metatarsi.

Spination

	F	P	T	Mt
I	d3	-	pl1	pl1
II	d3	-	-	dw3
III	d3	pl3d3rl1	pl2d4rl1v2-2-1	d1r11dw5
IV	d1	pl4d3rl1	pl2d5rl2v2-2-1	6disp dw5

Leg measurements

	F	P	T	Mt	t	Total
I	2.31	0.98	1.75	1.33	1.26	7.63
II	1.54	0.91	1.40	1.19	1.05	6.09
III	1.89	1.05	1.26	1.47	1.05	6.72
IV	2.31	1.19	1.96	2.31	1.26	9.03

Palp with pectinated claw turned inward over 45°. Tarsus provided with eight retrolateral spines.

Epigyne (Figs 2C–D, 4C–D, 5C): central depression with two dark areas; large kidney-shaped area on either side; inverted funnel-shaped pattern in front.

Distribution

Known from the Uzungwa and Uluguru Mts. in Tanzania (Fig. 16).

Palindroma aleykyela gen. et sp. nov.
urn:lsid:zoobank.org:act:D41FD227-07BF-4D3C-AA5D-C2571D88E741
Figs 6A–D, 7A–B, 16

Diagnosis

The males of *P. aleykyela* gen. et sp. nov. are easily recognized by large palpal patella and the conspicuous basal extension of the tegulum.

Etymology

The species name is an arbitrary combination of letters forming a noun in apposition and containing 'Kyela', the name of the type locality.

Material examined

Holotype

TANZANIA: ♂, 8 km NE of Kyela, 9°35' S, 33°48' E, 19 Nov.–1 Dec. 1991, pitfalls in miombo relict, R. Jocqué (MRAC 173610).

Other material

MALAWI: 1 ♂, Chintheche, 11°50' S, 33°13'E, Feb. 1977, R. Jocqué R. (MRAC 152373); 2 ♂♂, Nkhata Bay, Nkwazi evergreen forest, 11°36' S, 34°18' E, 2–20 Jan. 1978, R. Jocqué (MRAC 153031); 2 ♂♂, Nkhata Bay, Nkwazi evergreen forest, 11°36' S, 34°18' E, 23 Nov.–13 Dec. 1977, R. Jocqué

(MRAC 153248); 1 ♂, Nyika Plateau, near entrance gate on the Chelinda-Rumphi road, 10°40' S, 33°50' E, 3–22 Dec. 1981, secondary *Brachystegia* woodland with *Uapaca*, pitfalls, R. Jocqué (MRAC 156005); 1 ♂, as previous (MRAC 156064).

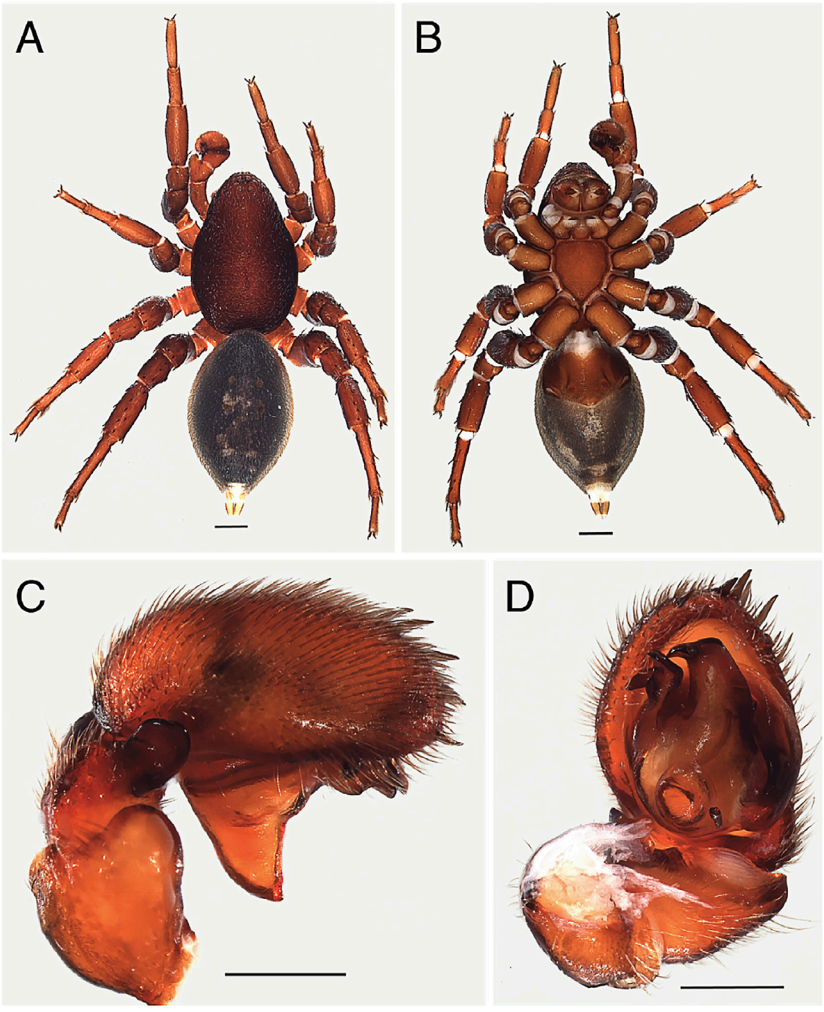

Fig. 6. *Palindroma aleykyela* gen. et sp. nov., holotype, ♂. **A**. Habitus, dorsal view. **B**. Idem, ventral view. **C**. Palp, retrolateral view. **D**. Idem, ventral view. Scale bars: A–B = 1 mm, C–D = 0.5 mm.

Description

Male (holotype)

Total length 9.87; carapace 4.97 long, 2.98 wide, narrowed to 1.42 in eye region.

Colour: carapace uniform dark brown with dispersed silvery hairs (Fig. 6A–B); chelicerae sternum and legs brownish orange; abdomen: dorsum grey with two pairs of reddish apodemes, white dispersed short setae, denser in posterior half, white spot in front of yellow spinnerets; sides grey with well delimited frontal reddish apodeme; venter pale grey, sclerotized and orange in front of epigastric fold.

Carapace coarsely granulate. Clypeus without erect setae.

Eyes: AME: 0.16; ALE: 0.20; ALE-ALE: 0.21; AME-ALE: 0.07; PME: 0.12; PLE: 0.18; PME-PME: 0.15; PME-PLE: 0.41. Clypeus 0.62 or 3.1 times width of ALE.

Chilum double, each sclerite 0.08 high, 0.16 wide; no setae. Sternum shield-shaped with sinuous sides, 2.00 long, 1.70 wide.

Chelicerae with mesodistal membranous extension. Endites swollen at base.

Legs: anterior tarsi fusiform, longer than metatarsi.

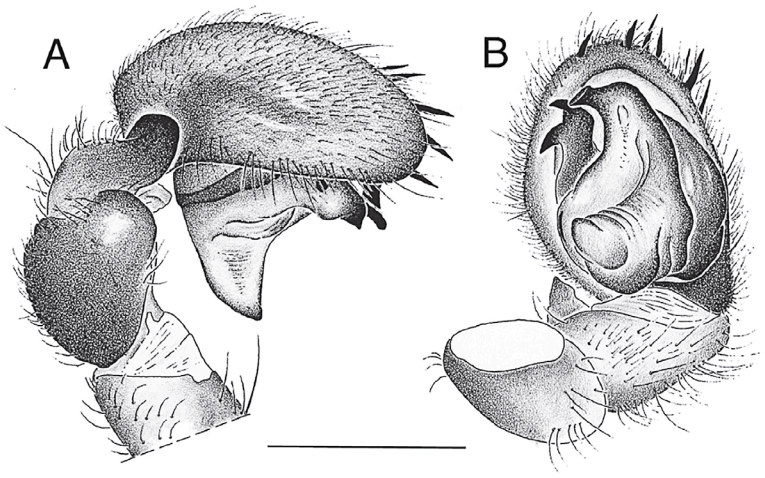

Fig. 7. *Palindroma aleykyela* gen. et sp. nov., ♂ (MRAC 153248). **A**. Palp, retrolateral view. **B**. Idem, ventral view. Scale bar = 1 mm.

Spination

	F	P	T	Mt
I	d2	-	pl1v1-1-2	dw3
II	d2	-	v1-1-2	dw2
III	d1-3	pl2d3rl1	pl3d4rl2v1-1-2	8dispdw6
IV	d1-3	pl2d3rl1	pl3d5rl2v1-1-2	10dispdw5

Leg measurements

	F	P	T	Mt	t	Total
I	2.38	1.19	1.96	1.26	1.40	8.19
II	2.17	1.19	1.68	1.12	1.05	7.21
III	2.31	1.33	1.47	1.47	1.05	7.63
IV	2.73	1.47	2.03	2.38	1.33	9.94

Epiandrum well developed, with two small, white, membranous spots.

Male palp (Figs 6C–D, 7A–B): patella large, with conspicuous mesolateral bulge; tibia with prolateral dorsal protrusion; RTA broad, short, with strongly sclerotized, rounded extremity; base strongly tapered to sharp extremity turned upward and outward; cymbium with seven prolateral spines in distal half; subtegulum strongly sclerotized; tegulum with large, pointed, basal extension, distally with short, dark, hooked process (HP); embolus short, curved, with rounded process at base.

Female

Unknown.

Distribution

Known from miombo woodland in northern Malawi and northern Tanzania (Fig. 16).

Palindroma avonova gen. et sp. nov.

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Figs 8A–D, 9A–C, 10A–D, 16

Diagnosis

The male of *P. avonova* gen. et sp. nov. is easily recognized by the characters of the palp: the swollen patella, the thick RTA, the ridged tegulum and the sickle shaped embolus. The female has a characteristic epigyne with longitudinal central depression separated from the posterior margin by a rectangular plate.

Etymology

The species name is an arbitrary combination of letters forming a noun in apposition and containing 'nova' (new) as the genus as well as the species are new.

Material examined

Holotype

TANZANIA: ♂, Muheza district, Manga Forest Reserve, 5°02' S, 38°47' E, Oct.–Dec.1994, Frontier Tanzania (ZMUC).

Paratypes

TANZANIA: 1 ♂, together with holotype (MRAC 244092); 2 ♂♂, 1 ♀, together with holotype (ZMUC); 5 ♂♂, 1 ♀, Muheza district, Marimba Forest Reserve, 5°01' S, 38°41' E, no date, Frontier Tanzania (ZMUC).

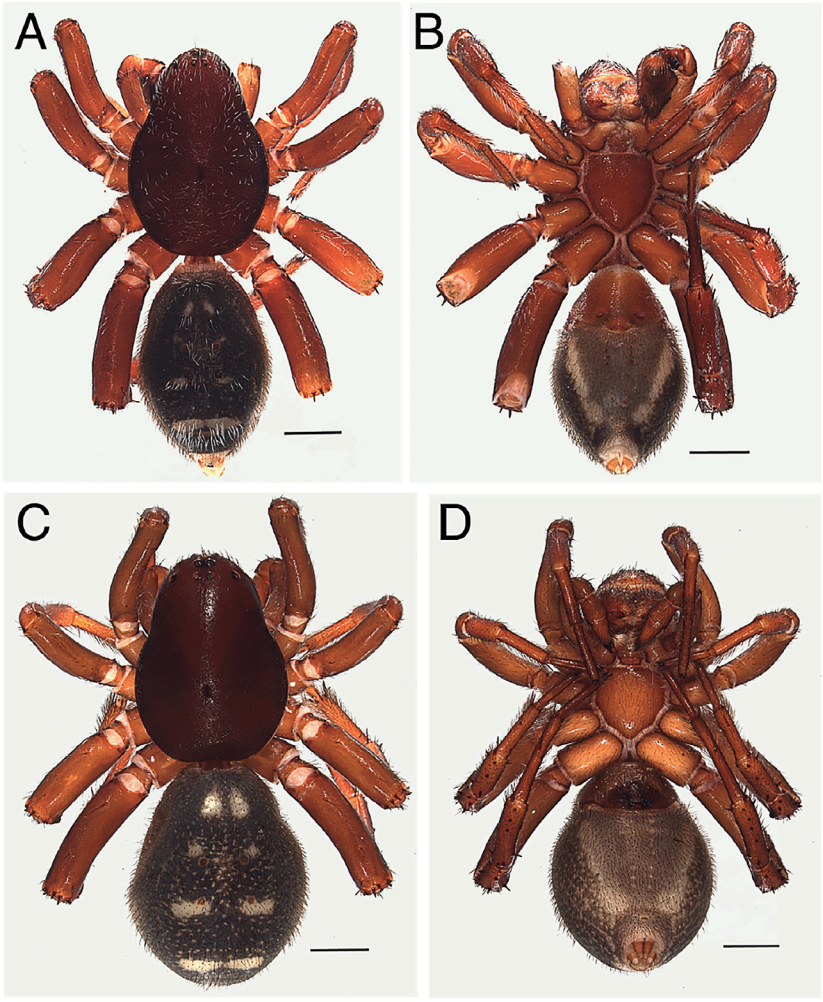

Fig. 8. *Palindroma avonova* gen. et sp. nov. A–B. Holotype, ♂. C–D. ♀ from Maringa Forest. **A**. ♂, habitus, dorsal view. **B**. Idem, ventral view. **C**. ♀, habitus, dorsal view. **D**. Idem, ventral view. Scale bars = 1 mm.

Other material

TANZANIA: 1 ♀, Coastal Region, Kazimzumbwi Forest Reserve, 6°57' S, 39°3' E, Jan.–Feb. 1991, Frontier Tanzania (ZMUC); 2 ♀♀, as previous; 1 ♂, as previous; 1 ♀, Pugu Forest Reserve, 9°59' S, 39°7' E, 25 Apr. 1981, leaf litter, K.M. Howell (MRAC 159097).

Description

Male (holotype)

Total length 7.60; carapace 3.83 long, 2.63 wide, narrowed to 1.28 in eye region.

Colour: Carapace dark brown with few silvery setae (Fig. 8A–B); chelicerae, sternum and legs medium brown; Mt I, II with white hairs. Abdomen: dorsum with white setae, denser in front and on posterior white bar; three pairs of white spots, one pair of adjacent white bars and a white bar in front of spinnerets; four apodemes well developed; sides dark grey; venter pale grey, well separated from sides by oblique white band on either side; sclerotized in front of epigastric fold; four rows of apodemes; spinnerets yellowish brown.

Carapace granulated.

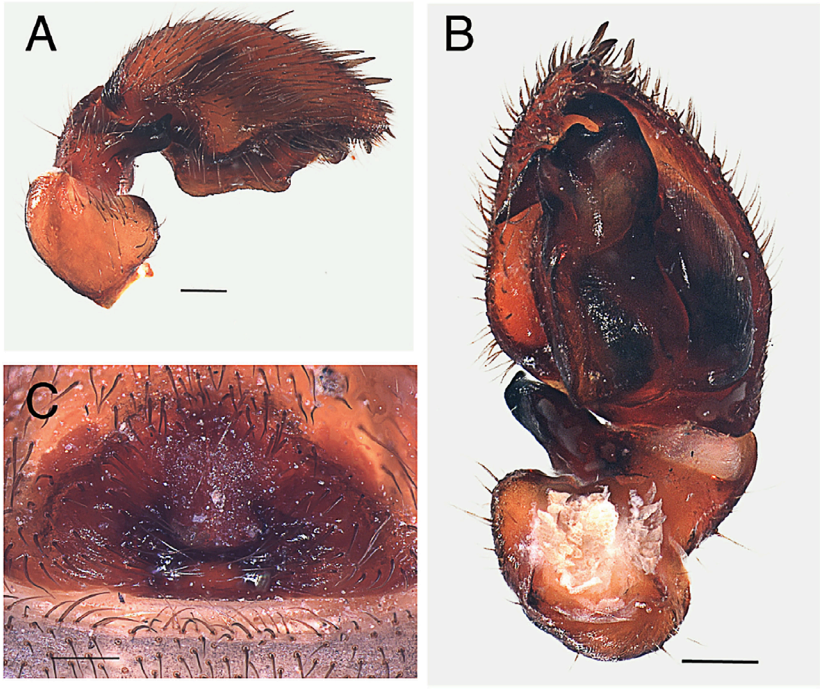

Fig. 9. *Palindroma avonova* gen. et sp. nov. A–B. Holotype, ♂. C. ♀ from Maringa Forest. **A**. ♂, palp, retrolateral view. **B**. Idem, ventral view. **C**. ♀, epigyne, ventral view. Scale bars = 0.2 mm.

Eyes: AME: 0.10; ALE: 0.14; ALE-ALE: 0.15; AME-ALE: 0.13; PME: 0.08; PLE: 0.13; PME-PME: 0.12; PME-PLE: 0.30. Clypeus 0.39 or 2.8 times width of ALE.

Chilum double, each sclerite 0.13 high, 0.20 wide; no setae. Chelicerae with distomesal membranous swelling. Sternum shield-shaped, 1.42 long, 1.28 wide.

Legs: anterior tarsi slightly longer than metatarsi.

Spination

	F	P	T	Mt
I	d3	-	-	dw2
II	d3	-	v3	dw2
III	d3+2*	pl3d1-2rl1	pl2d3rl1v2-2-2	d1dw5
IV	d3+3*	pl3d1-2rl1	pl3d5rl2v1-1-2	4dispdw5

* 3 long, slender setae + 2 or 3 short, thick, distal setae

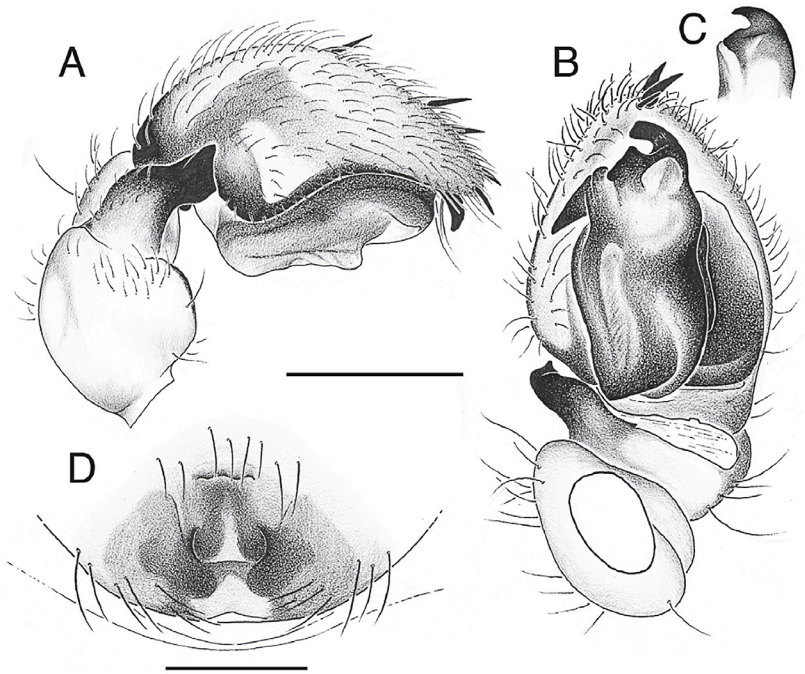

Fig. 10. *Palindroma avonova* gen. et sp. nov. A–B. Holotype, ♂. C. Paratype, ♂, from Marimba Forest. D. ♀ from Maringa forest. **A**. ♂, palp, retrolateral view. **B**. Idem, ventral view. **C**. Palp detail of paratype, enbolus, ventral view. **D**. ♀, epigyne, ventral view. Scale bars = 0.5 mm.

Leg measurements

	F	P	T	Mt	t	Total
I	1.68	0.84	1.54	0.98	1.05	6.09
II	1.61	0.84	1.26	0.98	0.70	5.39
III	1.75	0.84	1.33	1.12	0.70	5.74
IV	2.24	1.12	1.75	2.03	0.98	8.12

Male palp (Figs 9A–B, 10A–C): patella large, swollen; tibia with short, rounded dorsal process; RTA strongly sclerotized, short, thick, with truncated tip; cymbium with several spines in distal half; with basal swellings near dorsal tibial process and RTA; tegulum with longitudinal ventral ridge ending medially in poorly developed knob; embolus short, sickle shaped; MA strongly sclerotized, conical, pointing backward; subtegulum large, strongly sclerotized.

Female (paratype from Marimba Forest)
Total length 8.02; carapace 3.76 long, 2.63 wide, narrowed to 1.63 in eye region.

Colour: carapace dark brown without silvery setae (Fig. 8C–D); chelicerae, sternum and legs medium brown without white setae; abdomen: pattern as in male but without white setae and not sclerotized in front of epigastric fold but for epigyne. Further as in male.

Carapace: finely reticulated. Clypeus with dispersed setae.

Eyes: AME: 0.18; ALE: 0.20; ALE-ALE: 0.18; AME-ALE: 0.20; PME: 0.13; PLE: 0.16; PME-PME: 0.10; PME-PLE: 0.31. Clypeus 0.43 or 2.2 times width of ALE.

Chilum double, each sclerite 0.10 high, 0.26 wide; no setae. Sternum shield-shaped, 1.42 times as long as wide.

Legs:
Spination

	F	P	T	Mt
I	d3	-	-	dw2
II	d3	-	-	dw2
III	d2+1*	pl3d3	pl2d3rl1v1-1-1	d1dw5
IV	d2+3*	pl3d3rl1	pl5d2rl2v1-1-1	4dispdw5

* 2 long, slender setae + 1 or 3 short, thick, distal setae

Leg measurements

	F	P	T	Mt	t	Total
I	1.26	0.91	1.68	1.12	1.05	6.02
II	1.82	0.77	1.33	0.98	0.91	5.81
III	1.82	0.98	1.12	1.40	1.05	6.37
IV	2.45	1.05	1.96	2.10	1.19	8.75

Palp: claw with three teeth, turned inward over 45°. Tarsus provided with strong retrolateral spines.

Epigyne (Figs 9C, 10D): dark, fairly large central depression longitudinal, separated from posterior margin by transverse rectangular plate.

Distribution

Known from forest in Muheza District in Tanzania (Fig. 16).

Palindroma obmoimiombo gen. et sp. nov.
urn:lsid:zoobank.org:act:F5095BED-45CF-4480-B925-F86B7795A9B4
Figs 11A–E, 12A–D, 13A–B, 16

Diagnosis

The male of *P. obmoimiombo* gen. et sp. nov. is easily recognized by its colour, the inconspicuous cheliceral lamina and the characters of the palp: the unmodified patella, the presence of a dorsolateral tibial apophysis

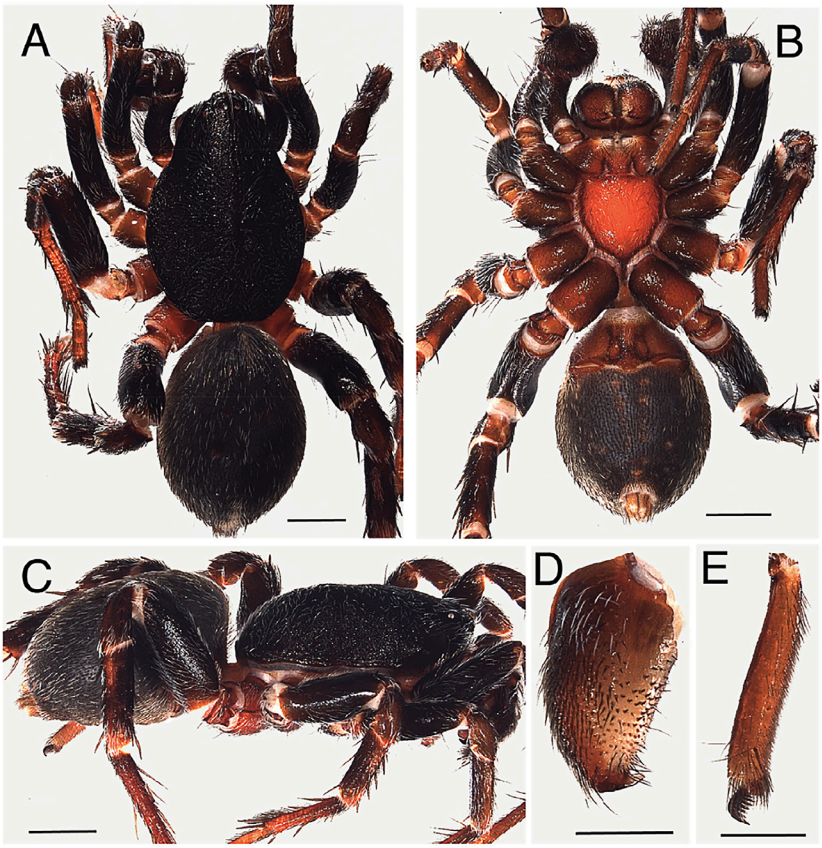

Fig. 11. *Palindroma obmoimiombo* gen. et sp. nov., paratype, ♂ (MRAC 241634). **A**. Habitus, dorsal view. **B**. Idem, ventral view. **C**. Idem, lateral view. **D**. Left chelicera, ventral view, showing mesal field of spinules. **E**. Tarsus 4, retrolateral view. Scale bars: A–C = 1 mm, D–E = 0.5 mm).

and a bifid RTA, the large subtegulum with ridges and posterior swelling and the thin embolus lying in a groove of the tegulum.

Etymology

The species name is an arbitrary combination of letters forming a noun in apposition and containing 'miombo', the type of woodland in which the type material was collected.

Material examined

Holotype

DEMOCRATIC REPUBLIC OF THE CONGO: ♂, Mikembo Sanctuary near Lubumbashi, 11°28' S, 27°39' E, 8 Nov. 2010, 1180 m, miombo woodland, by hand, R. Jocqué (MRAC 241633).

Paratype

DEMOCRATIC REPUBLIC OF THE CONGO: 1 ♂, Mikembo Sanctuary near Lubumbashi, 11°28' S, 27°39' E, 1–31 Oct. 2010, 1180 m, miombo woodland, by hand, Cemdika & Jenny (MRAC 241634).

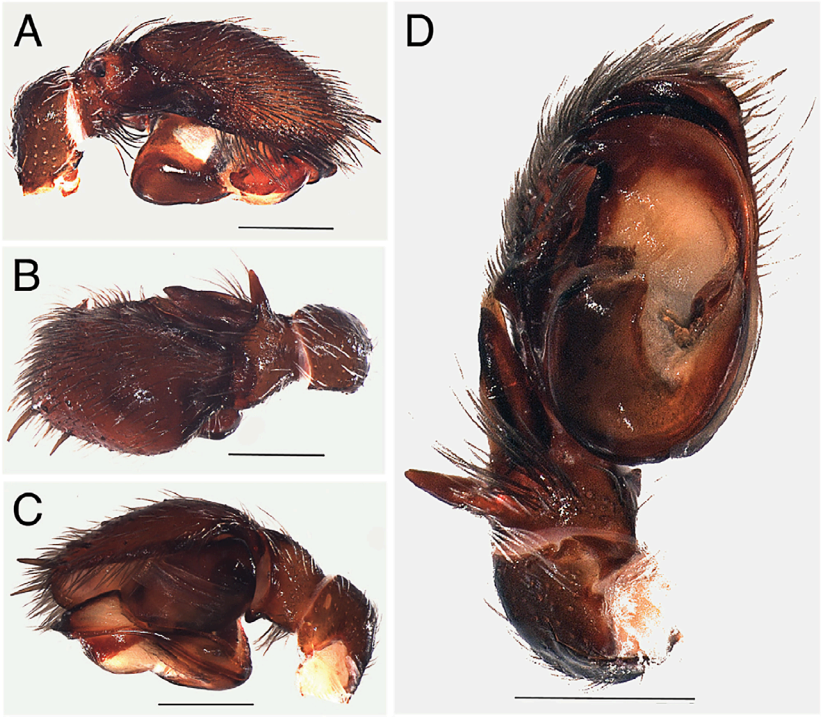

Fig. 12. *Palindroma obmoimiombo* gen. et sp. nov., holotype, ♂ (MRAC 241633). **A**. Palp, retrolateral view. **B**. Idem, dorsal view. **C**. Idem, prolateral view. **D**. Idem, ventral view. Scale bars = 0.5 mm.

Other material

None.

Description

Male (holotype)

Total length 7.46; carapace 3.91 long, 2.84 wide, narrowed to 1.56 in eye region.

Colour: carapace black with numerous silvery hairs (Fig. 11A–C); chelicerae dark brown with white setae in proximal half, medium brown with dark setae in distal half and white distomesal part (Fig. 11D); sternum orange; coxae and trochanters brownish orange, femora dark brown to black with numerous white setae; patellae and tibiae dark brown with few white setae; metatarsi and tarsi medium brown (Fig. 11E); abdomen dark grey with silvery setae, four reddish apodemes, three anastomosing pale spots in front of brownish spinnerets; sides dark grey with few silvery setae and reddish frontal apodeme; venter dark grey with two rows of small apodemes and a few near sides; orange in front of epigastric fold.

Carapace granulated, profile almost flat.

Eyes: AME: 0.13; ALE: 0.15; ALE-ALE: 0.31; AME-ALE: 0.08; PME: 0.13; PLE: 0.12; PME-PME: 0.10; PME-PLE: 0.25. Clypeus 0.64 or 4.3 times width of ALE.

Chilum double, each sclerite 0.10 high, 0.20 wide; no setae. Chelicerae with mesal side flat, with short spines; distomesal membranous swelling, absent. Sternum shield-shaped, 1.49 long, 1.42 wide, produced between posterior coxae.

Legs: anterior tarsi shorter than metatarsi.

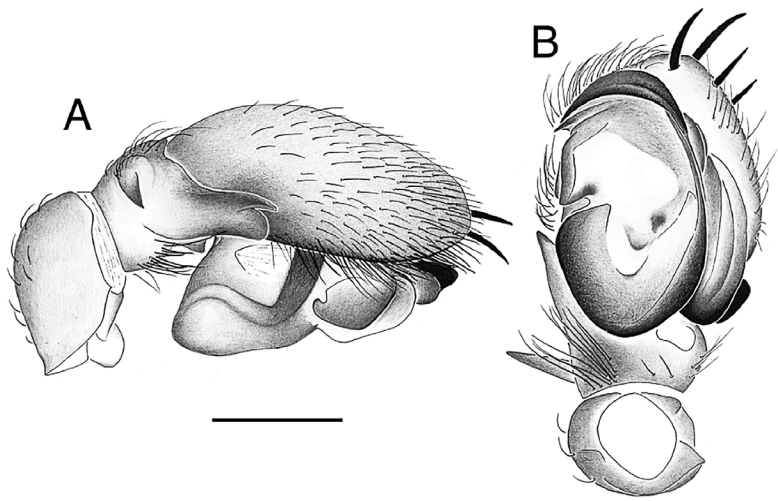

Fig. 13. *Palindroma obmoimiombo* gen. et sp. nov., holotype, ♂ (MRAC 241633). **A**. Palp, retrolateral view. **B**. Idem, dorsal view. Scale bars = 0.5 mm.

Spination

	F	P	T	Mt
I	d1	-	pl2	v2-2
II	d1	-	pl2	v2dw3
III	pl1d3	pl3d1rl1	pl3d3rl2v1-2-2	8disp dw5
IV	pl1d3	pl1d1rl1	pl3d3rl2v1-1-2	11disp dw5

Leg measurements

	F	P	T	Mt	t	Total
I	2.17	0.98	1.96	1.47	1.26	7.84
II	1.89	0.91	1.33	1.40	1.12	6.65
III	1.68	1.05	1.26	1.61	1.26	6.86
IV	2.24	1.19	1.75	2.31	1.40	8.89

Epiandrum well developed but without membranous patches.

Male palp (Figs 12A–D, 13A–B): patella not modified or enlarged; tibia with ventral bunch of long setae, sharp dorsolateral apophysis pointing outward, and RTA, concavity between the two; RTA distally bifid with pointed inferior part and lamellar, truncated superior part; cymbium with basolateral flange and seven prolateral spines; subtegulum large and prominent, with three longitudinal ridges, posterior part swollen; tegulum with two parts, centre membranous; distal part with transverse groove and knob pointing back; embolus thin and whip-shaped; distal extremity in tegular groove.

Female

Unknown.

Distribution

Known from Mikembo Sanctuary near Lubumbashi in the Democratic Republic of the Congo (Fig. 16).

Palindroma sinis gen. et sp. nov.

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Figs 14A–E, 15A–C, 16

Diagnosis

The male of *P. sinis* gen. et sp. nov. is easily recognized by the characters of the palp: the very simple RTA, which is a tiny protrusion, the short sharp, embolus and whitish setae on legs and abdomen.

Etymology

The species name is an arbitrary combination of letters forming a noun in apposition and containing 'sin' (Spanish for 'without') referring to the virtual absence of an RTA.

Material examined

Holotype

TANZANIA: ♂, Morogoro Region, Kimboza Forest Reserve, 7°01' S, 37°44' E, Jan.–Mar. 1994, Frontier Tanzania (ZMUC).

Paratypes

TANZANIA: 2 ♂♂, together with holotype (ZMUC); 2 ♂♂, together with holotype (MRAC 244093).

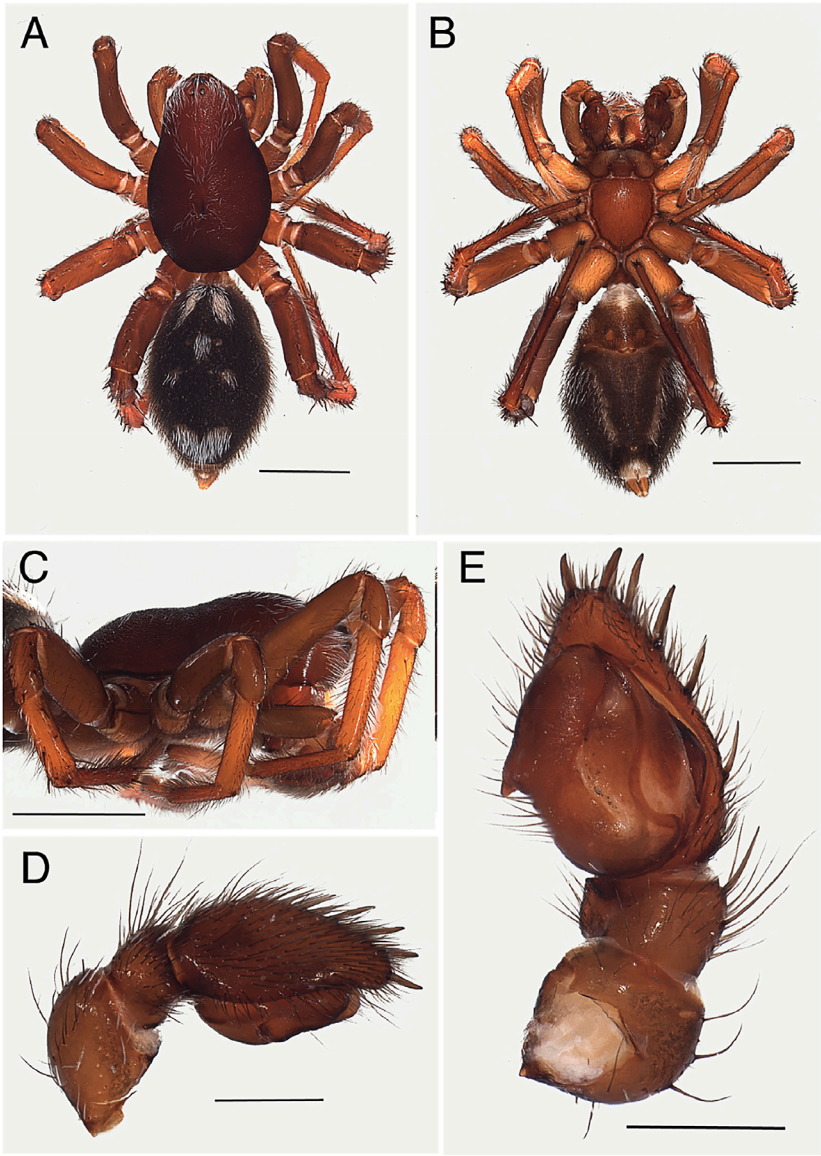

Fig. 14. *Palindroma sinis* gen. et sp. nov., holotype, ♂. **A**. Habitus, dorsal view. **B**. Idem, ventral view. **C**. Idem, lateral view. **D**. Palp, retrolateral view. **E**. Idem, ventral view. Scale bars: A–C = 2 mm, D–E = 0.5 mm.

Other material

TANZANIA: 1 ♂, Mandeni District, Genda-Genda South Forest, 5°33' S, 38°38' E, 29 Jun.–28 Sep. 1991, Frontier Tanzania (ZMUC); 2 ♂♂, Tanga District, Muneza Region, Magrotto Hill, 5°07' S, 38°45' E, Jul.–Sep. 1994, Frontier Tanzania (ZMUC).

Description

Male (holotype)

Total length 8.38; carapace 4.19 long, 2.56 wide, narrowed to 1.49 in eye region.

Colour: carapace dark chestnut brown with silvery setae in eye region and around fovea (Fig. 14A–C); chelicerae, sternum and legs medium orange-brown; anterior tarsi yellow; sparse dorsal white hairs on all T and Mt and on t II, dense on t I. Abdomen: dorsum dark grey with five small pale spots in anterior half, and large one in posterior half, all covered with white setae; four apodemes well developed; sides dark grey with sparse white hairs in anterior half; venter pale grey, well separated from sides by oblique pale band on either side; with two rows of apodemes; spinnerets yellowish brown.

Carapace finely reticulated, with conspicuous dip at level of fovea.

Eyes: AME: 0.13; ALE: 0.16; ALE-ALE: 0.20; AME-ALE: 0.15; PME: 0.13; PLE: 0.15; PME-PME: 0.10; PME-PLE: 0.30. Clypeus 0.46 or 2.4 times width of ALE.

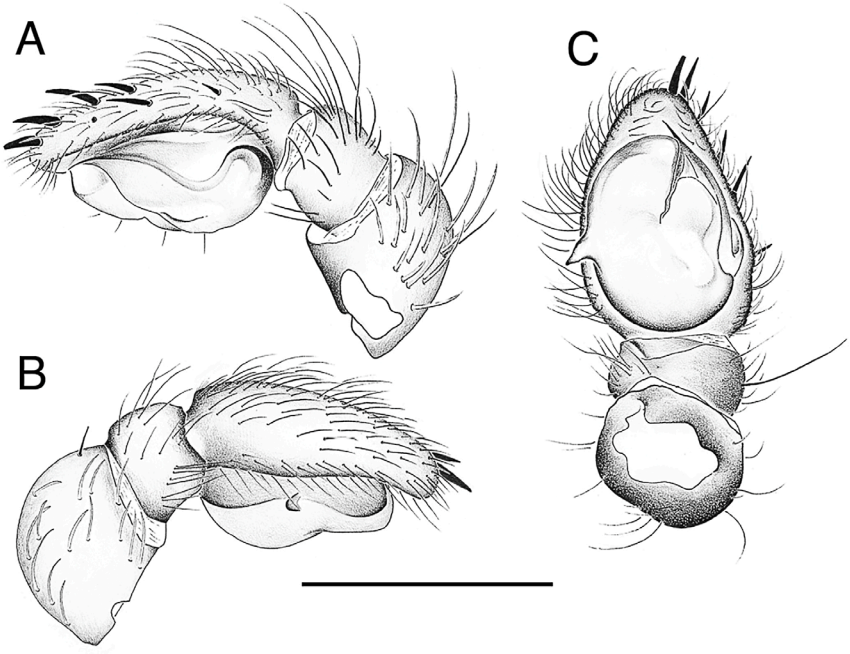

Fig. 15. *Palindroma sinis* gen. et sp. nov., holotype, ♂. **A**. Palp, prolateral view. **B**. Idem, retrolateral view. **C**. Idem, ventral view. Scale bar = 1 mm.

Chilum double, each sclerite 0.10 high, 0.25 wide; no setae. Chelicerae with distomesal membranous swelling. Sternum shield-shaped, 1.56 long, 1.35 wide.

Legs: anterior tarsi shorter than metatarsi.

Spination

	F	P	T	Mt
I	pl1d2	-	v1-1-1	dw2
II	pl1d2	-	v1-1-1	dw3
III	d2rl1	pl2d3rl1	pl3d3rl1v2-2-2	4dispdw5
IV	d2rl1	pl2d3rl1	pl3d5rl2v2-2-2	9dispdw5

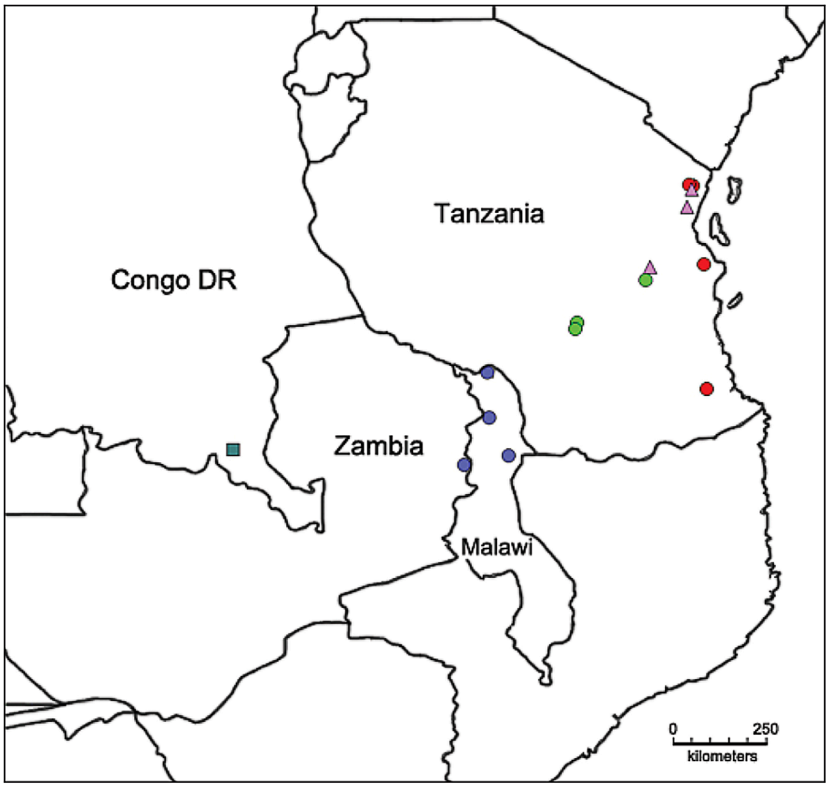

Fig. 16. Distribution map of *P. avonova* gen. et sp. nov. (●), *P. aleykyela* gen. et sp. nov. (●), *P. morogorom* gen. et sp. nov. (●), *P. obmoimiombo* gen. et sp. nov. (■) and *P. sinis* gen. et sp. nov. (▲).

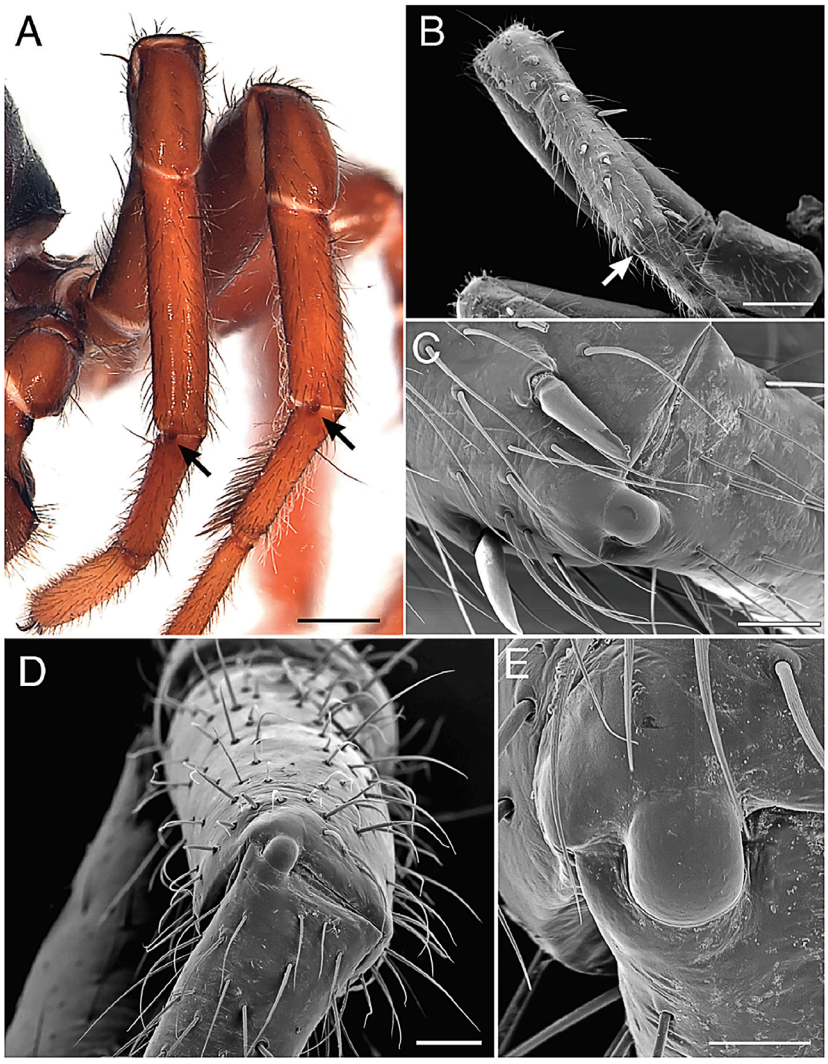

Fig. 17. *Palindroma morogorom* gen. et sp. nov. **A**. Left legs I and II, frontal view; arrows indicate tibial process. **B**. Left leg III, tibia and metatarsus, dorsal view. **C**. Detail of previous. **D**. Left leg II, tibia and metatarsus, dorsal view. **E**. Detail of previous. Scale bars: A–B = 0.5 mm, C–D = 100 mm, E = 50 mm.

Leg measurements

	F	P	T	Mt	t	Total
I	2.10	0.91	1.75	1.68	1.47	7.91
II	1.96	0.91	1.33	1.54	1.26	7.00
III	1.96	1.05	1.40	1.89	0.98	7.28
IV	2.38	1.12	1.96	2.73	1.33	9.52

Abdomen with well developed epiandrum; posterior margin with two semi-circular extensions, each preceded by tiny pit with membranous bottom.

Male palp (Figs 14D–E, 15A–C): RTA a tiny protrusion; tegulum with longitudinal cleft; prolateral part with sinuous sperm duct visible in transparency, retrolateral part with sharp, back-pointing knob; embolus short, straight, with sharp tip pointing forward. Without MA and conductor.

Female

Unknown.

Distribution

Known from Morogoro Region, Tanga District and Muheza District in Tanzania (Fig. 16).

Discussion

The tibial process

All representatives of *Palindroma* gen. nov. were found to have a characteristic tibial process (Fig. 17A–D) on all legs of both sexes. It consists of a rounded lip-shaped extension of the distal, dorsolateral margin of the tibia, fitting in a shallow pouch on the proximal dorsal margin of the metatarsus. Scanning of other zodariids showed that the character appears to be present in all representatives of the family. It is obvious in almost all species, except in some taxa provided with a single femoral organ. In all observed species (see appendix) the process is situated near the prolateral side of the dorsal margin of the tibia (Fig. 17A). The relative size of the structure varies. It is particularly well developed in *Palindroma* gen. nov., but fairly small although still obvious in *Cryptothele* L. Koch, 1872 (Fig. 18C–D) as can be observed in fig. 2A of Ramirez *et al.* (2014). It is clearly visible in the other basal genera, for instance in *Cyrioctea* (Fig. 18E), *Lachesana* Strand, 1932 (Fig. 19A) and *Cybaeodamus* Mello-Leitão, 1938 (see Ramirez 2014: fig. 52e). It is conspicuous in representatives of the Storeninae: *Amphiledorus* Jocqué & Bosmans, 2001 (Fig. 18A), *Mallinella* Strand, 1906 (Fig. 19B), *Holasteron* Baehr, 2004 (Fig. 18F). It is present and distinct in genera with a dual femoral organ: *Asceua* Thorell, 1887 (Fig. 18B), *Suffasia* Jocqué, 1991 and *Suffrica* Henrard & Jocqué, 2015 (Fig. 19C), but has been overlooked by Henrard & Jocque (2015). However, it is less conspicuous in the other taxa with a femoral organ where it is situated under the rim of the tibia and not on it as in the other taxa: *Diores* Simon, 1893 (Fig. 20E–F), *Zodarion* Walckenaer, 1826 (Fig.19D), *Ranops* Jocqué, 1991 (Fig. 19F). In some of the Zodariinae it is partly hidden and difficult to discern when the leg is not bent at the tibia-metatarsus joint: *Microdiores* Jocqué, 1987 (Fig. 19E), *Parazodarion* Ovtchinnikov, Ahmad & Gurko, 2009 (Fig. 20C–D), *Trygetus* Simon, 1882 (Fig. 20A–B). The structure is absent in those taxa that have been regarded as putative sister-groups like Amaurobiidae (Fig. 21A), Agelenidae (Fig. 21B), Penestomidae (Fig. 21D), Corinnidae (*Procopius* sp., *Cambalida* sp.) Gnaphosidae (*Haplodrassus* sp.) or even in Titanoecidae (Fig. 21C). Another kind of tibial processes occurs in a few other families where a small process on both sides of the dorsal tibial rim is present. These have been called 'condyles' by Ramirez (2014: fig. 44b). However, they are obviously not homologous with the tibial process described here, since a tibial process and condyles may occur together on the rim of the tibia as in *Cryptothele* (Fig. 18C–D). The structure as found in Zodariidae appears to be a unique synapomorphy and its presence in basal zodariid taxa,

e.g., *Cyrioctea* (Fig. 18E) and *Lachesana* (Fig. 19A), thus confirms the position of these genera in that family. This remarkable feature may be of great help for the identification of zodariid fossils or of spider leftovers containing a single intact leg, in vertebrate stomach contents for instance.

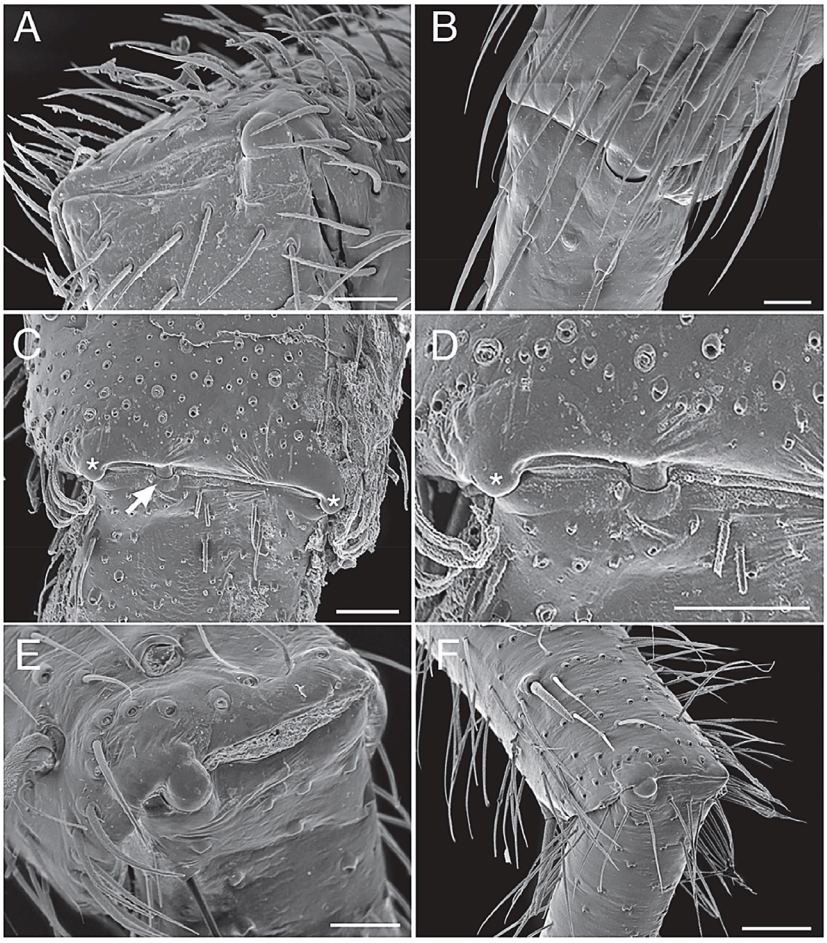

Fig. 18. A. *Amphiledorus* sp., juvenile, right tibia I. **B**. *Asceua* sp., ♂, right tibia and metatarsus IV. **C**. *Cryptothele doreyana* Simon, 1890, ♀, left tibia and metatarsus II. **D**. Idem, detail. **E**. *Cyrioctea marken* Platnick & Jocqué, 1992, ♂, left tibia and metatarsus III. **F**. *Holasteron aciculare* Baehr, 2004, ♂, left tibia and metatarsus III. Scale bars: A, E = 50 µm, B = 20 µm, C–D, F = 100 mm. Arrow shows tibial process, asterisk indicates condyle.

Distribution

In Jocqué (2009) and Jocqué *et al*. (2013) it was argued that the spider fauna of miombo woodlands has a character of its own and hardly overlaps with that of montane or coastal forests. The presently known distribution of the genus *Palindroma* gen. nov. is therefore somewhat puzzling. It is the first cryptotheline genus that is found in miombo woodland but it also occurs in coastal forest, even if

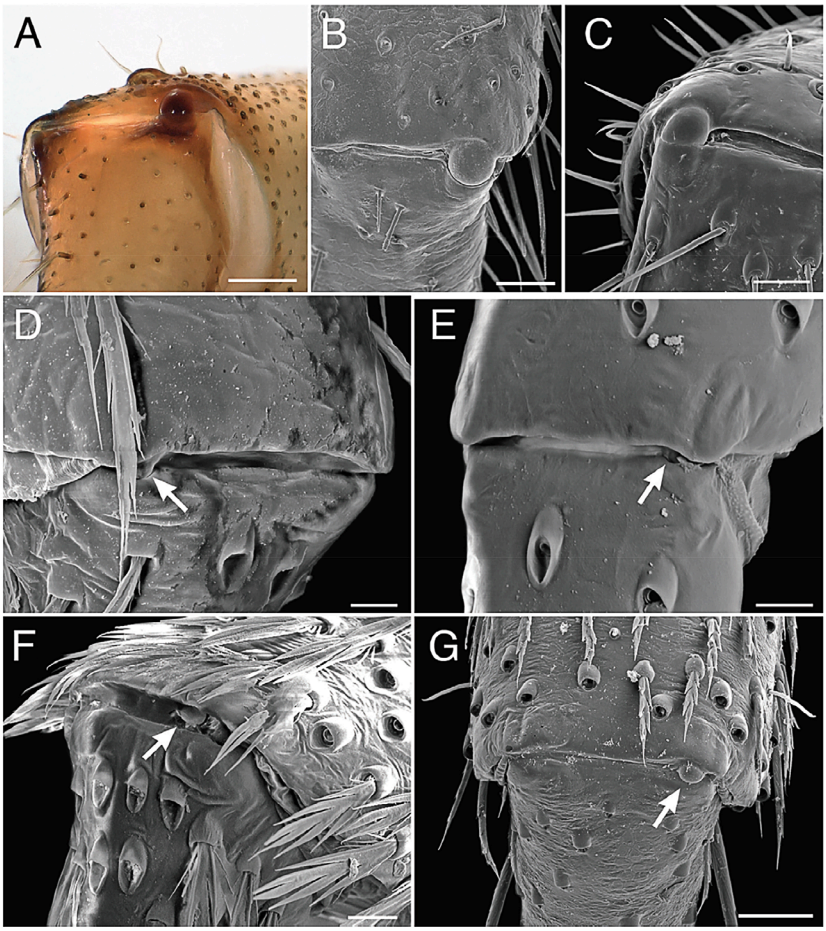

Fig. 19. A. *Lachesana blackwalli* (O. Pickard-Cambridge, 1872), ♂, right tibia and metatarsus III, dorsal view. **B**. *Mallinella* sp., ♂, right tibia and metatarsus II. **C**. *Suffrica gus* Henrard & Jocqué, 2015, ♂, left tibia and metatarsus I. **D**. *Zodarion nesiotes* Denis, 1965, ♀, right tibia and metatarsus I. **E**. *Microdiores* sp., ♂, right tibia and metatarsus I. **F**. *Ranops caprivi* Jocqué, 1991, ♂, right tibia and metatarsus II. **G**. *Diores milloti* Jocqué, 1990, ♀, right tibia and metatarsus I. Scale bars: A = 100 mm, B, G = 50 mm, C, F = 20 mm, D–E = 10 mm. Arrow shows tibial process, asterisks indicate condyles.

abstraction is made of *P. obmoimiombo*, which may belong to another genus as explained above. The vast miombo biome, 3.6 million km² (against 2.3 million km² for rainforest), is spread across eleven

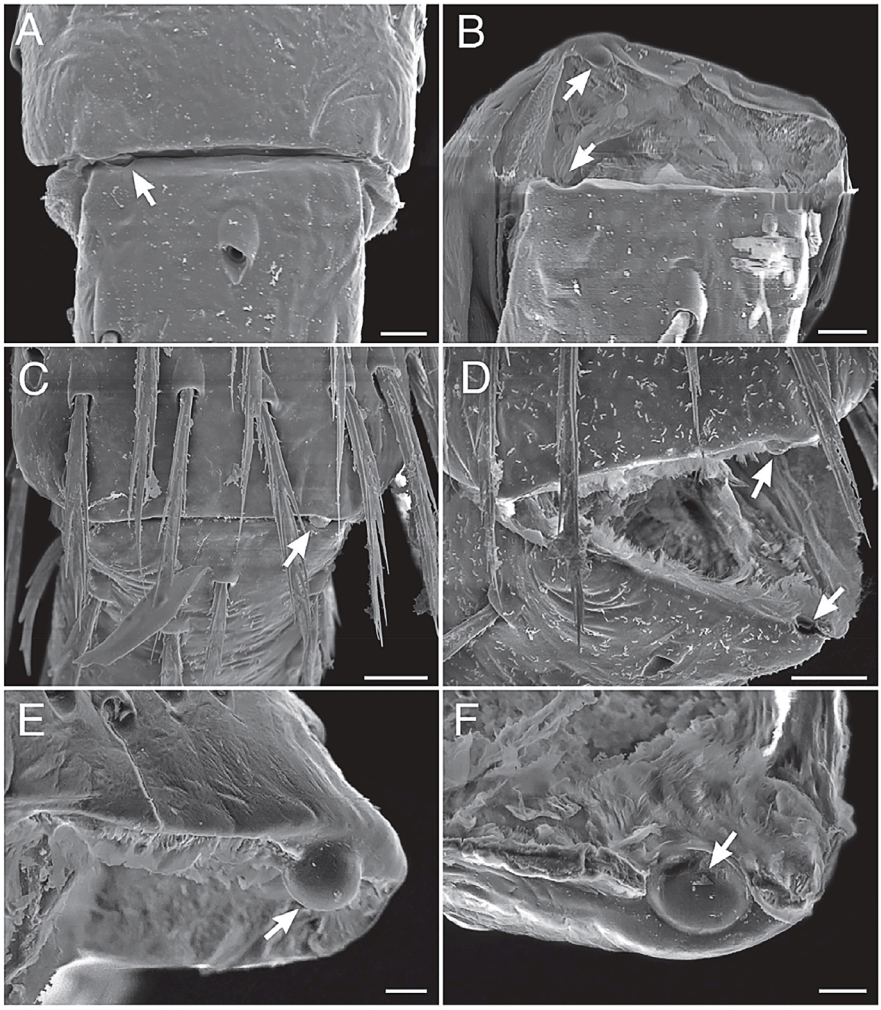

Fig. 20. A. *Trygetus sexoculatus* (O. Pickard-Cambridge, 1872), ♂, left tibia-metatarsus joint III. **B**. As previous, left tibia-metatarsus joint II; arrows indicate tibial process and metatarsal concavity. **C**. *Parazodarion raddei* (Simon, 1889), ♂, right tibia-metatarsus joint III; arrow indicates tibial process. **D**. As previous, right tibia-metatarsus joint II; arrows indicate tibial process and metatarsal concavity. **E**. *Diores poweri* Tucker, 1920, ♀, right tibia-metatarsus joint IV; arrow indicates tibial process. **F**. Idem, detail; arrow indicates metatarsal concavity. Scale bars: A–B, E–F = 10 mm, C–D = 20 mm.

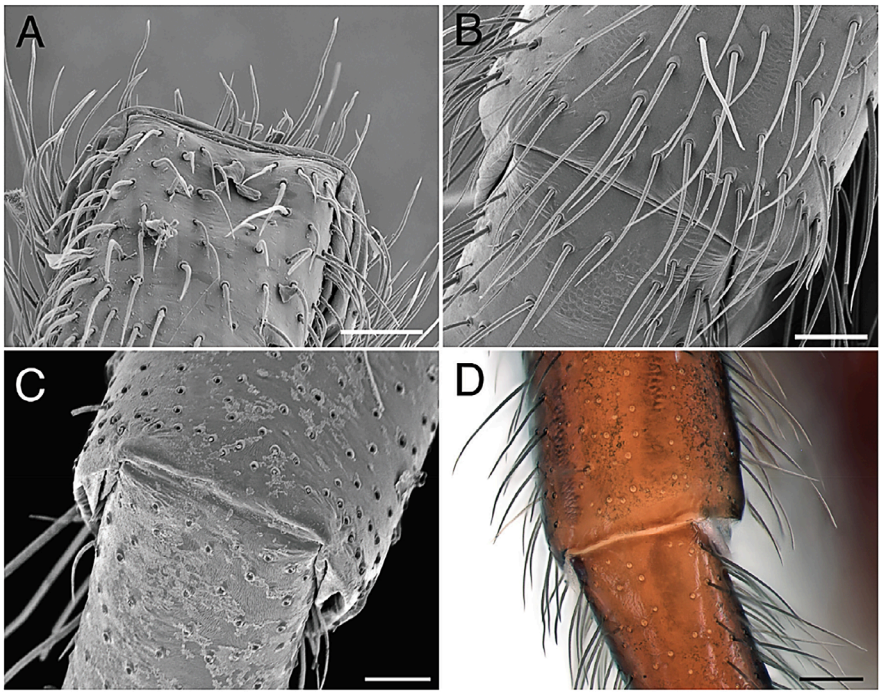

Fig. 21. A. *Amaurobius fenestralis* (Ström, 1768), ♀, base of right metatarsus 3. **B**. *Coelotes terrestris* (Wider, 1834), ♂, right tibia-metatarsus joint III. **C**. *Nurscia albomaculata* (Lucas, 1846), ♂, right tibia-metatarsus joint III. **D**. *Penestomus montanus* Miller, Griswold & Haddad, 2010, ♀, right tibia-metatarsus joint I. Scale bars: A–B, D = 100 mm, C = 50 mm.

countries in southern Africa and is probably the least studied ecoregion of the continent. More detailed studies of the ecoregion will doubtlessly discover more species of the genus and most likely species that are closely related to *P. obmoimiombo* gen. et sp. nov.

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We are grateful to Nikolaj Scharff (ZMUC) for the loan of material and to Alain Reygel for the splendid drawings. Additional material was provided by Barbara Baehr, Stefan Foord, Charles Griswold, Charles Haddad, Robert Raven and Milan M. Rézàc. The senior author has reached the age of 69 years, a perfect diagonal palindrome, and grabbed this occasion to create a genus of which the name was inspired by that term. This paper is publication BRC 340 of the Biodiversity Research Center (Université Catholique de Louvain). This work was supported by the FRIA (Fonds pour la Formation à la Recherche dans l'Industrie et dans l'Agriculture). We thank Robert Bosmans and an anonymous referee for comments on the first draft.

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Appendix

Comparative material studied

Amaurobius fenestralis (Ström, 1768) (Fig. 21A), ♀, Belgium, Tervuren, under bark of tree, 1 Feb. 2011, hand catch, A. Henrard rec.

Amphiledorus sp. (Fig. 18A), sub adult ♂, Portugal, Alentejo, 1 Apr. 2005, hand catch, M. Rézàc leg.

Asceua sp. (Fig. 18B), ♂, Phillipines, Luzon Island, Quezon Province, Mt. Banahaw de Luchan, 5.25 km WSW of Luchan, elev. 1279 m, 14°05.217' N, 121°31.036' E, forest, 17–22 May 2011, propylene glycol pitfall traps, H. Wood, M. Yngente, N. Choussou Poludouri, C. Griswold & V. Knutson rec., PH0029, CASENT-9042498.

Coelotes terrestris (Wider, 1834) (Fig. 21B), ♂, Belgium, Marchin, Porche de Roiseux, on litter near cliffs, 13 Sep. 2014, hand catch, A. Henrard rec.

Cryptothele doreyana Simon, 1890 (Fig. 18C–D), ♀, New Caledonia, Aoupinie top camp, 21°11' S, 165°18' E, 2–3 Nov. 2001, 850 m, sieved litter, berlesate 1060, G.B. Montheit (Queensland Museum QM90506).

Cyrioctea marken Platnick & Jocqué, 1992 (Fig. 18E), ♂, South Africa, Limpopo prov., 10 Jun. 2009, pitfall traps, S. Foord rec., 12N/B4.

Diores milloti Jocqué, 1990 (Fig. 19G), ♀, Madagascar, 17–20 Jan. 2009, general collecting day and night, CASENT 9031122.

Diores poweri Tucker, 1920 (Fig. 20E–F), ♀, South Africa, Free State Province, Bloemfontein, National Botanic Gardens, grassland, 29°02' S, 26°12' E, 28 Nov. 2012, Pitfall tarps, C. Haddad rec.

Holasteron aciculare Baehr, 2004 (Fig. 18F) (QM).

Lachesana blackwalli (O. Pickard-Cambridge, 1872) (Fig. 19A), ♂, Israel, Dead Sea, MRAC 169819.

Mallinella sp. Thailand (Fig. 19B) (ZMUC).

Microdiores sp. (Fig. 19E), ♂, Democratic Republic of the Congo, Mikembo, miombo woodland, Uapaca forest, 11°28' S, 027°39' E, 26 Oct. 2010, pitfall traps, R. Jocqué & M. Hasson rec., MRAC 234392.

Nurscia albomaculata (Lucas, 1846) (Fig. 21C), ♂, France, Adrets de l'Estérel, under stone, 17 Jul. 2013, hand catch, A. Henrard rec.

Parazodarion raddei (Simon, 1889) (Figs 20C–D), ♂, United Arab Emirates, Wadi Wurayah farm, 25°24' N, 56°17' E, 13 Jan.–2 Mar. 2009, Malaise trap, A. Van Harten rec., MRAC 233874.

Penestomus montanus Miller, Griswold & Haddad, 2010 (Fig. 21D), ♀ paratype, Lesotho, Qachas Nek district, near Ha Mphahama, stone ridge, under rocks, 1820 m, 30°05.520' S, 28°35.746' E, active search, C. Haddad rec., SNCAP-2006/1535.

Ranops caprivi Jocqué, 1991 (Fig. 19F), ♂, South Africa, Free State Province, Bloemfontein, National Botanical Gardens, 29°02' S, 26°12' E, 12 Oct. 2012, C. Haddad leg.

Suffrica gus Henrard & Jocqué, 2015 (Fig. 19C), ♂, Tanzania, Tanga, East Usambara Mts, Amani, 5°5.7' S, 38°38' E, 950 m, 28 Oct.–9 Nov. 1995, pitfalls, C. Griswold, N. Scharff & D. Ubick leg., MRAC.

Trygetus sexoculatus (O. Pickard-Cambridge, 1872) (Fig. 20A–B), ♀, Egypt, Sinai, 50 km E of Suez, 31 Mar. 2000, M. Alderweireldt rec., MRAC 209667.

Zodarion nesiotes Denis, 1965 (Fig. 19D), ♀, Fuerteventura, near "La Pared", under stones, 9 Apr. 2011, hand catch, A. Henrard leg.

CHAPTER III

THE DUAL FEMORAL ORGAN CLADE

During the examination of materials used for morphological character scoring, some taxa appeared new to science and were found to be characterized by remarkable combinations of features which have not been documented in spiders so far (Henrard and Jocqué 2015; Jocqué and Henrard 2015a; 2015b; 2015c). Among the spiders that are specialized on the predation of ants, the zodariids possessing a specialized gland on the femur form a well-supported group: the Zodariinae *sensu* Jocqué (1991a). Until recently, the femur of these spiders was thought to bear a unique femoral organ. However, during our morphological scoring, a dual femoral organ has been found for the first time on all legs in the newly described taxa *Suffrica* Henrard & Jocqué, 2015 and *Suffascar* Henrard & Jocqué, 2017 but also in the genera *Asceua* Thorell, 1887 and *Suffasia* Jocqué, 1991. A preliminary morphology-based phylogenetic analysis was then performed in order to test whether zodariids sharing the dual femoral organ are part of the same group (DF) as the Zodariinae *sensu* Jocqué (1991a), which is called here "single femoral organ clade" (SF), and whether they form a separate monophyletic group.

The present chapter is based on two published papers :

***Sub-chapter IIIa – The new genus* Suffrica**

Henrard A. & Jocqué, R. (2015). On the new Afrotropical genus *Suffrica* with discovery of an abdominal gland and a dual femoral organ (Araneae, Zodariidae). *Zootaxa* 3972(1): 1–25. doi:10.11646/zootaxa.3972.1.1

***Sub-chapter IIIb – The new genus* Suffascar**

Henrard, A. & Jocqué, R. (2017). The new ant-eating spider genus *Suffascar* (Araneae, Zodariidae) endemic to Madagascar: a considerable extension of the dual femoral organ clade. *Invertebrate Systematics* 31: 519-565. doi:10.1071/IS16064

SUB-CHAPTER IIIA

– ON THE NEW AFROTROPICAL GENUS SUFFRICA

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On the new Afrotropical genus *Suffrica* with discovery of an abdominal gland and a dual femoral organ (Araneae, Zodariidae)

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Abstract

A new genus, *Suffrica*, is described from Tanzania and Kenya. It contains three new species occurring in the Eastern Arc Mountains and the adjacent Mkomazi Game Reserve: *S. exotica*, *S. chawia* and *S. gus*. They are characterized by a remarkable combination of features which has not been documented in spiders so far: a pair of femoral organs on each leg, a gland on the dorsal side of the abdomen in both sexes and a dorsal abdominal groove in males. A dual femoral organ appears to occur in species of the genus *Suffasia* Jocqué, 1991 and *Asceua* Thorell, 1887. The discovery of a new African genus close to *Suffasia* is remarkable since the latter genus is known only from Asia.

Key words: *Asceua*, Eastern Arc, relic distribution, spider glands, *Suffasia*

Introduction

The genus *Suffasia* Jocqué, 1991 has a critical position in the Zodariidae because it is morphologically intermediate between the classic subfamilies Zodariinae and Storeninae (Jocqué 1991, 1992). It contains the main diagnostic characters of both subfamilies: the preening brushes with chisel-shaped setae typical for the Storeninae and the femoral organs characteristic for the Zodariinae. For that reason the two subfamilies were united into the Zodariinae (Jocqué 1992). Apart from the unusual combination of the characters mentioned, *Suffasia* is further recognized by the presence of one or a double tooth on the promargin of the chelicerae; most other representatives of the subfamily Zodariinae lack such teeth. It is also the only genus in the Zodariidae in which species have been described with an abdominal modification in the male (e.g. *S. tumegaster* presents a ventral boss, Jocqué 1992).

The genus was considered endemic to Asia (hence its name) and currently contains seven species from India, Nepal and Sri Lanka. However, many new species await description (Dankittipakul, pers. comm.) and it is likely that the genus, with its present definition, will reach the high species diversity of genera like *Mallinella* Strand, 1916 and *Asceua* Thorell, 1887.

Samples from East Africa yielded three remarkable new spider species. These spiders resemble *Suffasia* in having a similar femoral organ and comparable habitus and eye disposition, but differ in having a dorsal abdominal gland in both sexes and the abdomen with a dorsal groove in males. This combination of features is unique among zodariids and prompted the description of a new genus. The discovery of a new African genus apparently closely related to *Suffasia* comes as a great surprise, as the Zodariidae of the African continent have been inventoried in some detail. Possibly an even greater revelation was the dual femoral organ we found during the description of the three *Suffrica* species. It was subsequently observed in *Suffasia*, *Asceua* and some undescribed species from Madagascar (pers. obs.) but not in any other zodariids.

Material and methods

Specimens were observed, drawn and measured with a WILD M 10 stereomicroscope. Details of the female

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genitalia and male palps were observed with a Zeiss Stemi 2000 stereomicroscope. Measurements and photographs of the habitus, details of mouthparts, detached male palps and female genitalia were taken with a Leica MZ16 using the LAS automontage software (ver. 3.8). The female genitalia were dissected and digested with pancreatin and then immersed in 75% ethanol.

For SEM photos, specimens were dried in hexamethyldisilazane (36h), gold coated and examined and photographed with a JEOL 6480 LV scanning electron microscope. Some specimens were processed for SEM after having been used in a DNA extraction protocol (Macherey-Nagel protocol). After the DNA extraction process, the specimens (or remaining pieces) were considerably cleaner, making them more suitable for SEM observation (see Paquin & Vink 2009). Types are deposited in the Royal Museum for Central Africa, Tervuren, Belgium (MRAC), in the Zoological Museum of the University of Copenhagen (ZMUC) and in the California Academy of Sciences, San Francisco (CAS).

All measurements are in mm; ranges (e.g. of size) are given in brackets.

Abbreviations

ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
AME	anterior median eyes
AW	anterior width
C	conductor
CAS	California Academy of Sciences, San Francisco
d	dorsal
DTA	dorsal tibial apophysis
dw	distal whorl
E	embolus
F	femur
H	height
L	length
MA	median apophysis
MOQ	median ocular quadrangle
MRAC	Musée Royal de l'Afrique Centrale (Tervuren, Belgium)
MS	median spinnerets
Mt	metatarsus
O	opening (gland)
P	patella
pl	prolateral
PLE	posterior lateral eyes
PLS	posterior lateral spinnerets
PME	posterior median eyes
RTA	retrolateral tibial apophysis
S	setae
SEM	scanning electron microscope
t	tarsus
tot	total length
T	tibia
TA	tegular apophysis
v	ventral
W	width
ZMUC	Zoological Museum of the University of Copenhagen

Taxonomy

***Suffrica* gen. nov.**
Figs 1–96

Diagnosis. Members of the genus *Suffrica* resemble *Suffasia* and *Asceua* in having a pair of femoral organs without barbed setae on each leg (Figs 17–20), a similar eye disposition and teeth on both cheliceral margins. They are distinguished by the narrow, domed cephalothorax (Figs 2, 7), the cheliceral promargin with two well separated slanting teeth, the proximal one larger (Fig. 41), a dorsal abdominal gland (Figs 8, 9, 37, 47, 76–81) and the dorsum of the abdomen with a groove in males (Figs 6, 26, 65).

Etymology. *Suffrica* is a contraction of *Suffasia* and Africa. The gender is feminine.

Type species. *Suffrica exotica* **sp. nov.**

Description. Small spiders (1.9–2.9 mm). Carapace (Figs 3, 6, 7, 36, 38) narrow, oval (L/W = 1.5–1.7) and domed (L/H = 1.92–2.24), with smooth to slightly reticulated teguments, almost devoid of hairs; widest at level of coxae II–III, narrowed anteriorly to about 0.70 times maximum width in males and 0.75 times maximum width in females (cephalic width measured at level of PLE centers). Cervical grooves not marked.

Colour (Figs 1–3, 25–27, 64–66): carapace medium to dark brown; chelicerae and mouthparts dark brown; sternum medium brown; abdomen dorsum uniform dark in females, with two longitudinal lighter stripes in male, anteriorly with small, central lighter brown spot at level of abdominal gland, venter uniform grey, darker towards sides.

Eyes in two rows: anterior row straight, procurved as seen from in front (Figs 3, 36), posterior row strongly procurved. All eyes rounded and subequal. MOQ longer than wide, wider at the back than in front. Clypeus straight, height about 5 times diameter of ALE, with dispersed short setae.

Chilum single, superior margin wider than inferior one, slightly protruding in the center (Fig. 3). Chelicerae not fused (Fig. 36); intercheliceral triangle absent; promargin with two slanting teeth, the proximal one larger and retromargin with one small, sharp tooth (Fig. 41); fangs short and sharp, slightly curved. Labium roughly quadrangular with rounded distal margin, hardly narrowed at base (Fig. 39). Endites roughly triangular, strongly converging, distally with special asymmetric setae (Fig. 40); palps directed straight forward. Sternum slightly longer than wide, shield-shaped with slightly rounded sides, provided with triangular extensions corresponding with coxal concavities and with intercoxae.

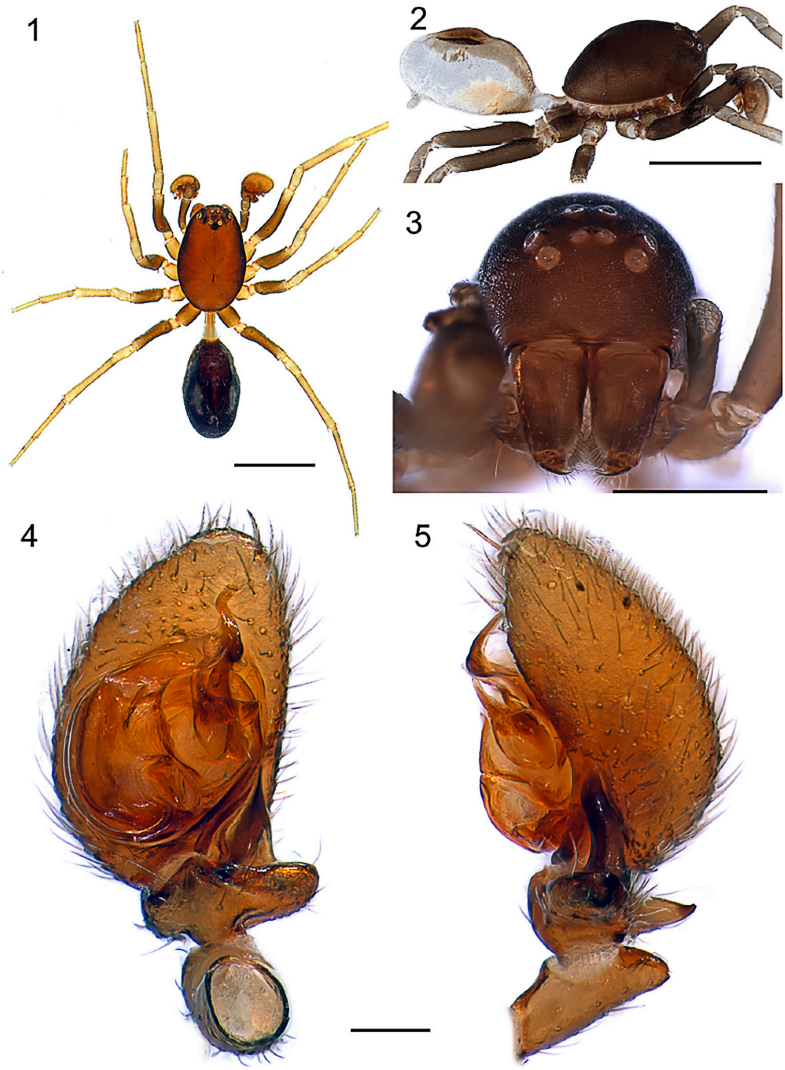
Legs slender. Formula 4123 or 4132. Three-clawed (Fig. 83), median one smooth, lateral ones medially pectinated as in most Zodariids. Spination reduced but a few dorsal spines on femora and some small ventral spines on tibiae and metatarsi; distal ones on metatarsi ramified (Fig. 82). Preening brush with short chisel-shaped setae on metatarsi II and III (Fig. 82). Femoral organ double, on prolateral and retrolateral face of all legs, with smooth conical hairs and numerous small pores in a shallow circular depression (Figs 17–20). Tarsal organ simple hole on distal edge of elevated plate (Fig. 84), located on proximal part of tarsi.

Abdomen oval. Dorsum in both sexes anteriorly with oval gland outlet with coarsely granulated tegument, tiny gland openings and smooth setae (Figs 8, 9, 37, 47, 76–81); internal view shows perforated oval area, with numerous pits, larger ones corresponding to the base of smooth setae, smaller ones accommodating the outlets of flat, oval glands (Figs 80, 81); abdomen provided in males with scutum covering ¾ of surface, with central longitudinal groove delimited by shallow ridges (Figs 2, 6, 26, 35, 65, 75). Tracheal spiracle procurved, widened to rounded opening at extremities (Fig. 22); just in front of spinnerets; fairly wide, around 0.25 times maximum width of abdomen. Males with four spinnerets (Fig. 21), females with six (Fig. 49). ALS (Figs 22, 23, 51–53), conical, biarticulate, with two major ampullate gland spigots in the center and five (in males) or six (in females) aciniform gland spigots around the former. PLS small, with eight aciniform gland spigots in female (Fig. 50), two in male (Fig. 24). MS absent in males, reduced in females with one aciniform gland spigot (Fig. 50). Colulus represented by a few setae. Sperm pore a wide slightly procurved slit.

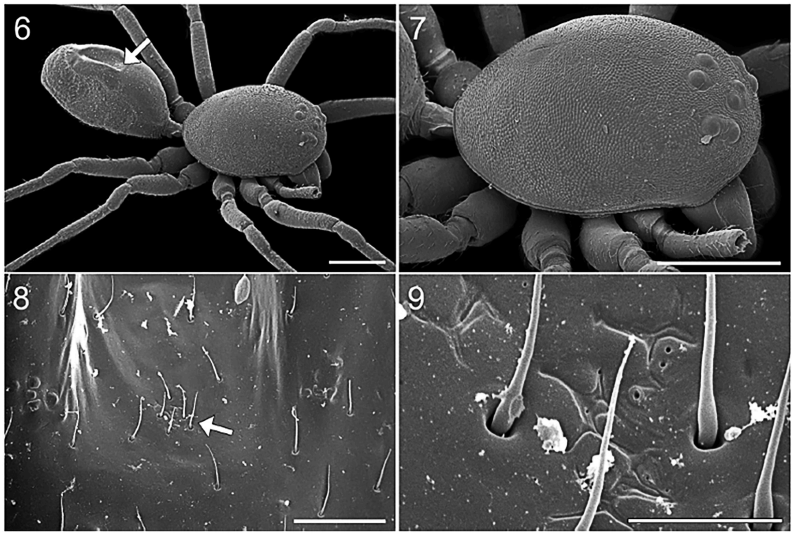
Female palp with some strong prolateral spines on conical tarsus, with pectinated claw turned inwards over nearly 45°, without patch of chemosensitive setae (Figs 48, 85).

Male palp with patella provided with rounded dorsal extension, tibia with both DTA and RTA: DTA short, conical and sturdy, RTA with two parts: one fairly long anterior lamellar extension pointing forwards and one rounded with transparent window, the two parts separated by plate-shaped concavity (Figs 16, 42, 86). Cymbium domed, with basal concavity accommodating lamellar extension of RTA; with patch of chemosensitive setae;

embolus originating on posterior part of tegulum (Fig. 10), cylindrical and grooved, long, curved, flexible, with small tooth at some distance from tip (Figs 12, 88); extremity truncated and folded (Fig. 12); MA (Figs 11, 45, 87) complex with different appendages: one prolateral, long, sharp and curved forwards and two retrolateral, rounded and stout; distal tegular apophysis harpoon-shaped (Fig. 13); conductor with basal groove accommodating embolus and distal part provided with curved, flat apophysis (Figs 11, 14, 15, 44, 89).



FIGURES 1–5. *Suffrica chawia* **sp. n.** (1) Male paratype (MRAC 221982), habitus, dorsal view: (2) Male paratype (MRAC 233020) used for DNA extraction, habitus lateral view; (3) as previous carapace and chelicerae, anterior view; (4) Male palp (MRAC 221982), ventral view; (5) as previous, retrolateral view. Scale bars (1, 2) = 1 mm; (3) = 0.5 mm; (4, 5) = 0.1 mm.



FIGURES 6–9. *Suffrica chawia* **sp. n.**, male paratype (MRAC 221982), SEM views. (6) habitus, dorso-lateral view, arrow points to the glandular outlet; (7) prosoma, dorso-lateral view; (8) abdominal glandular structure (arrow), dorsal view; (9) as previous, detail. Scale bars (6, 7) = 0.5 mm; (8) = 50 µm; (9) = 10 µm.

Epigyne (Figs 30, 34, 54, 55, 60, 69, 72, 90, 91) anteriorly with two membranous funnels (Figs 58, 94) connected to sinuous sclerotized copulation ducts, leading to poorly defined spermathecae (Figs 31, 56, 57, 62, 73, 92, 93). Funnels internally with numerous biarticulate glands (Figs 59, 63, 95), here called "lollipops", opening through small holes on the outside (Figs 55, 61, 91).

Distribution. *Suffrica* is found in the Eastern Arc Mountains and the adjacent Mkomazi Game Reserve (Fig. 96).

***Suffrica chawia* sp. nov.**
Figs 1–24, 96

Type material. Holotype. KENYA: ♂: Taita Hills, Chawia Forest, 3°29'S 38° 20'E, 1550m, 22.II.2004, pitfalls, Spanhove T. & Chovu M. (MRAC 221964).

Paratypes. 3♂: KENYA, Taita Hills, Chawia Forest, 3°29'S 38°20'E, 1550m, 22.II.2004, pitfall traps, Spanhove T. & Chovu M. (MRAC 221946); 5♂: as previous, (MRAC 221959); 1♂: as previous (MRAC 221972); 2♂: as previous, 24. II.2004 (MRAC 221975); 3♂: as previous, 22.II.2004 (MRAC 221982); 3♂: as previous (MRAC 222000); 1♂: as previous, 24.V.2004 (MRAC 233025); 1♂: as previous (MRAC 233020).

Diagnosis. The male of this species is recognized by the finely reticulate carapace, the leg spination, the abdomen with a deep furrow and a reduced glandular outlet (Figs 6, 8, 9) and details of the palp such as the smooth conductor with blunt tip (Figs 11, 15).

Etymology. The species name is a noun in apposition taken from the only forest in the Taita Hills where the species was collected.

Description. Male (Holotype). Total length 2.92, carapace 1.37 long, 0.90 wide and 0.64 high. **Carapace** (Figs 1–3, 6, 7) finely reticulated, medium brown, darker along margin and with very faint radiating striae; chelicerae and chilum pale brown; sternum brownish orange; legs: coxae and femora brown, remainder yellow. **Clypeus** 0.25 high. **Eyes** AME: 0.05: ALE: 0.05; PME: 0.07; PLE: 0.06; AME–AME: 0.02; AME–ALE: 0.07; PME–PME: 0.04; PME–PLE: 0.12. MOQ: width 0.13 in front, 0.18 at the back; 0.21 long.

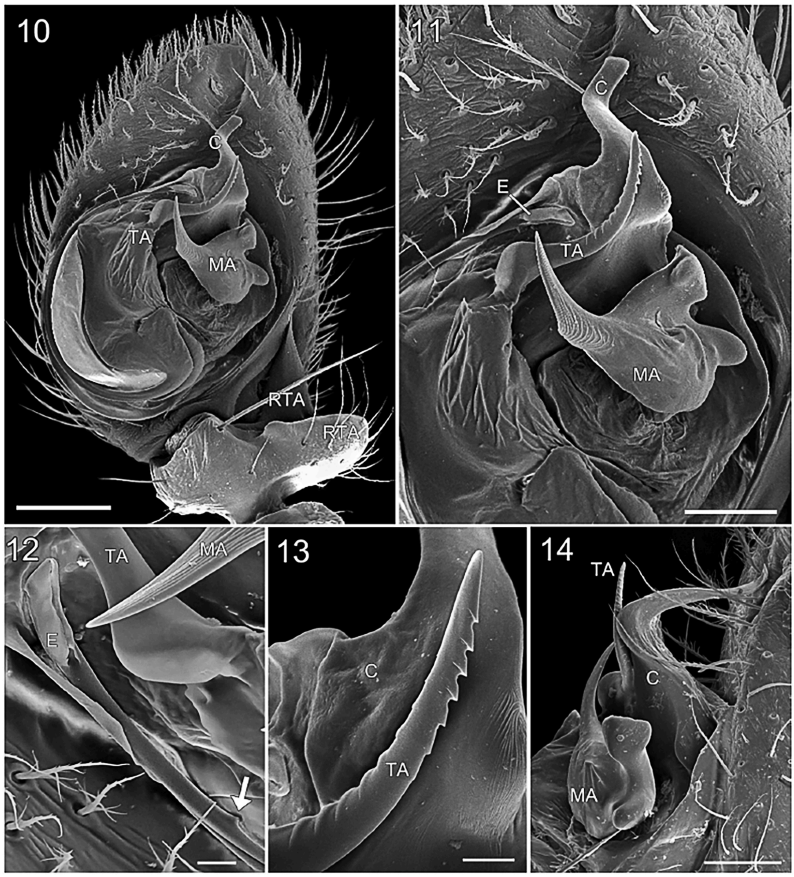
Chilum 0.10 high, 0.13 wide; trapezoidal, inferior margin concave.

Sternum: 0.74 long, 0.57 wide.

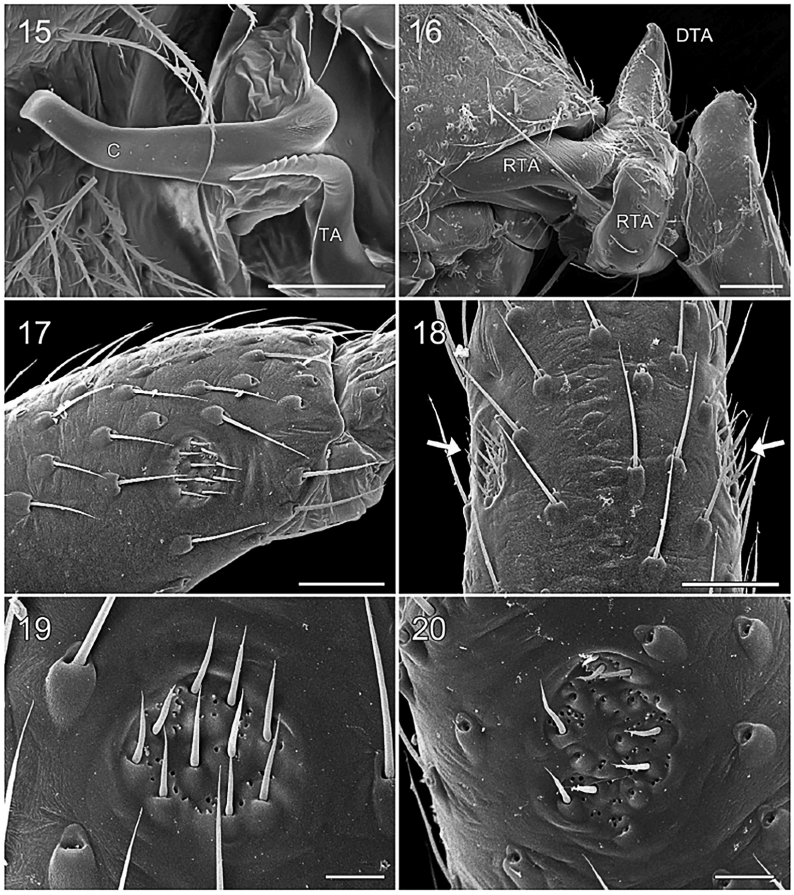
Legs: spination: Fe: I d1 II d1 III d1 IV d2; T (all spines at distal extremity): III pl1 v2 IV pl1 v2; Mt (all spines at distal extremity): I v(pl)1 II v(pl)2 III dw4 IV dw4. All femora with prolateral and retrolateral femoral organs (Figs 17–20).

Leg measurements:

	Fe	P	T	Mt	t	tot
I	0.85	0.29	0.70	0.61	0.51	2.96
II	0.71	0.29	0.48	0.51	0.38	2.37
III	0.71	0.22	0.48	0.58	0.35	2.34
IV	0.92	0.29	0.67	0.80	0.35	3.03



FIGURES 10–14. *Suffrica chawia* **sp. n.**, male paratype (MRAC 221982), SEM views of palp; (10) palp, ventral view; (11) as previous, detail; (12) detail of embolus, ventral view, arrow indicates the small tooth-like extension; (13) tegular apophysis, detail of the extremity, ventral view; (14) detail of the median apophysis and conductor, prolateral view. **C** = conductor, **E** = embolus, **MA** = median apophysis, **TA** = tegular apophysis. Scale bars (10) = 100 µm; (11, 14) = 50 µm; (12, 13) = 10 µm.



FIGURES 15–20. *Suffrica chawia* **sp. n.**, male paratype (MRAC 221982), SEM views. (15) palp conductor, anterior view; (16) palp apophyses, retrolateral view; (17) femur II, distal part, prolateral view; (18) femur III, distal part, dorsal view, arrows indicate the dual femoral organ; (19) femoral organ on leg I, dorso-prolateral view; (20) as previous, leg IV. **C** = conductor, **DTA** = dorsal tibial apohysis, **RTA** = retrolateral tibial apophyis, **TA** = tegular apophysis. Scale bars (15–18) = 50 µm; (19, 20) = 10 µm.

Abdomen: dorsum with brown scutum in front of deep central longitudinal dorsal furrow provided anteriorly with faint gland outlet with few small needle like setae and tiny pores (Figs 6, 8, 9); on both sides with grey, smooth ridge; sides sepia; venter pale. **Spinnerets** (Figs 21–24) white.

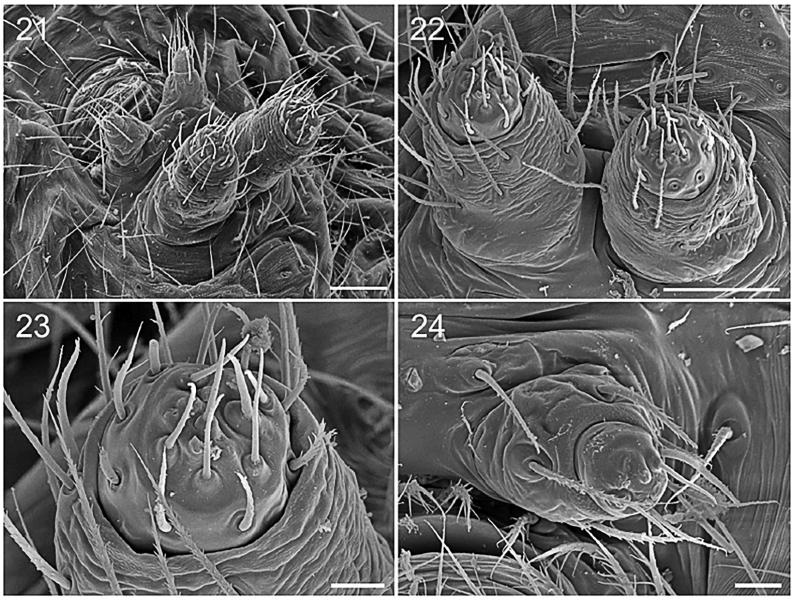
Palp. (Figs 4, 5, 10–16). Patella almost twice as high as long; tibia with conical DTA, its extremity slightly bent forward, and RTA with anterior blade-shaped extension and posterior, simple, roughly rectangular retrolateral apophysis separated from anterior extension by deep groove; ventrally with conspicuous long, straight seta; cymbium strongly domed, with distal ventral groove accommodating the conductor and deep basal, retrolateral concavity accommodating the anterior tibial extension of the RTA; embolus with small tooth halfway near the flat and obliquely truncated tip, enveloped in basal part of conductor; the latter large, with flat, slightly curved distal

part and blunt tip; MA large, with sharp, straight, ridged prolateral prong and two short retrolateral lobes, posterior one rounded, anterior one truncated and stout; distal tegular apophysis (TA) with long, slender, serrated prong.

Female. Unknown.

Variation. Total length of males (n=16) varies between 2.5 and 3.0. The pale area along the ridges on the abdominal dorsum varies from a narrow longitudinal patch to a broad reniform spot.

Distribution. Only known from Chawia Forest in the Taita Hills, Kenya (Fig. 96).



FIGURES 21–24. *Suffrica chawia* **sp. n.**, male paratype (MRAC 221982), spinnerets; (21) general overview of spinnerets, ventral oblique view; (22) anterior lateral spinnerets, anterior view; (23) as previous, detail; (24) posterior lateral spinnerets, anterior view. Scale bars (21, 22, 24) = 50 µm; (23) = 10 µm.

***Suffrica exotica* sp. nov.**
Figs 25–63, 96

Type material. Holotype. TANZANIA: ♂: Mkomazi Game Reserve, Ibaya, Igire Ridge, 1200m, 3°58'S 37°46'E, 24.XI.1994, litter of dry forest, crest of ridge, Russell-Smith A. (MRAC 241686).

Paratypes. TANZANIA: 1♀, together with holotype (MRAC 241686); 33♂ 17♀: same data as holotype (MRAC 215732).

Diagnosis. Specimens of *S. exotica* differ from the other species in having a dorsal spine on T III and IV. The males differ by the well developed abdominal glandular outlet (Fig. 53), the shape of the RTA and DTA which is less high (Figs 29, 33, 42), the thicker MA (Fig. 45) and the conductor which is angled rather than curved, with a rounded tip and provided with a small triangular extension (Fig. 44).

Etymology. The species is an adjective referring to the unexpected presence of relatives of *Suffasia* in Africa.

Description. Male (Holotype). Total length 2.56, carapace 1.21 long, 0.81 wide and 0.54 high. **Carapace** (Figs 25, 36, 38) finely reticulated, medium brown, with small darker area in front of fovea; chelicerae and chilum pale brown; sternum brownish orange; legs: coxae and femora pale brown, remainder yellow. **Clypeus** 0.15 high. **Eyes** AME: 0.07: ALE: 0.08; PME: 0.08; PLE: 0.08; AME–AME: 0.03; AME–ALE: 0.02; PME–PME: 0.03; PME–PLE: 0.07. MOQ: width 0.13 in front, 0.17 at the back; 0.20 long.

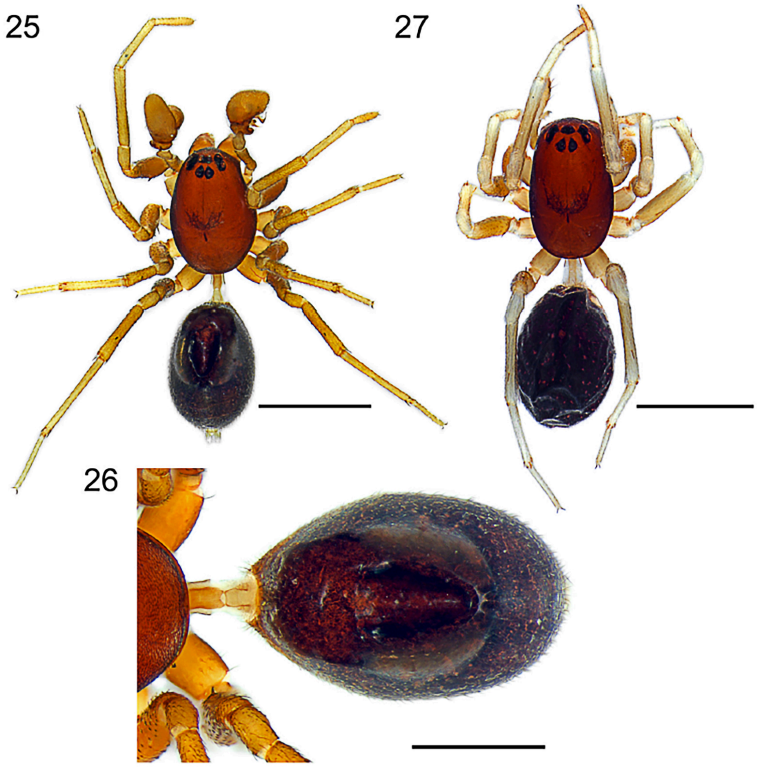
Chilum 0.07 high, 0.10 wide; trapezoidal, inferior margin straight.

Sternum: 0.59 long, 0.56 wide.

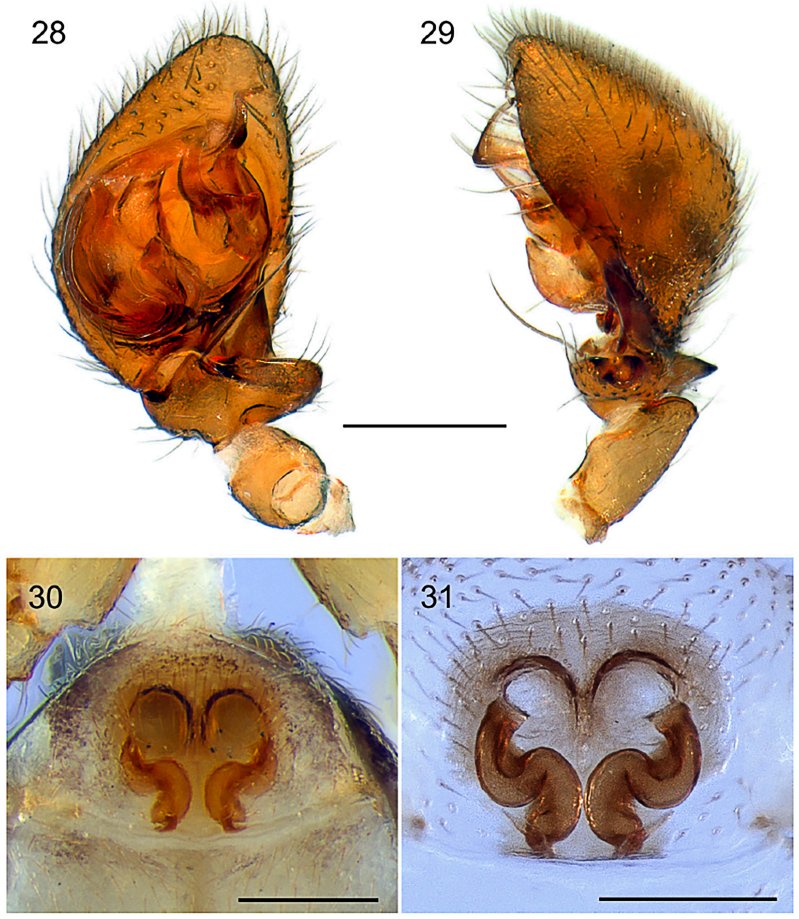
Legs: spination: Fe: I d2 II d2 III d2 IV d2; T (all spines except dorsal at distal extremity): III d1 middle pl1 v2 IV d1 at 2/3 pl1 v2; Mt (all spines at distal extremity): I v(pl)1 IIv(pl)2 III dw4 IV dw4.

Leg measurements:

	Fe	P	T	Mt	t	tot
I	0.78	0.27	0.69	0.60	0.45	2.79
II	0.60	0.24	0.51	0.48	0.36	2.19
III	0.54	0.27	0.54	0.51	0.33	2.19
IV	0.81	0.27	0.75	0.75	0.51	3.09



FIGURES 25–27. *Suffrica exotica* **sp. n.**; (25) male paratype (MRAC 215732), habitus, dorsal view; (26) as previous, detail of the abdomen; (27) female paratype (MRAC 241686), habitus, dorsal view. Scale bars (25, 27) = 1 mm; (26) = 0.5 mm.



FIGURES 28–31. *Suffrica exotica* **sp. n.**, male palp and female genitalia; (28) male paratype (MRAC 215732), palp, ventral view; (29) as previous, retrolateral view; (30) female paratype (MRAC 241686), epigyne, ventral view; (31) female paratype (MRAC 215732), vulva, after digestion, dorsal view. Scale bars (28, 29) = 0.1 mm; (30, 31) = 0.2 mm.

Abdomen (Figs 26, 37): dorsum with brown scutum in front of deep central longitudinal dorsal furrow provided anteriorly with faint gland outlet with few small needle like setae, on both sides with light grey, smooth ridge. Sides sepia, venter somewhat darkened towards the back. **Spinnerets** as in *S. chawia*.

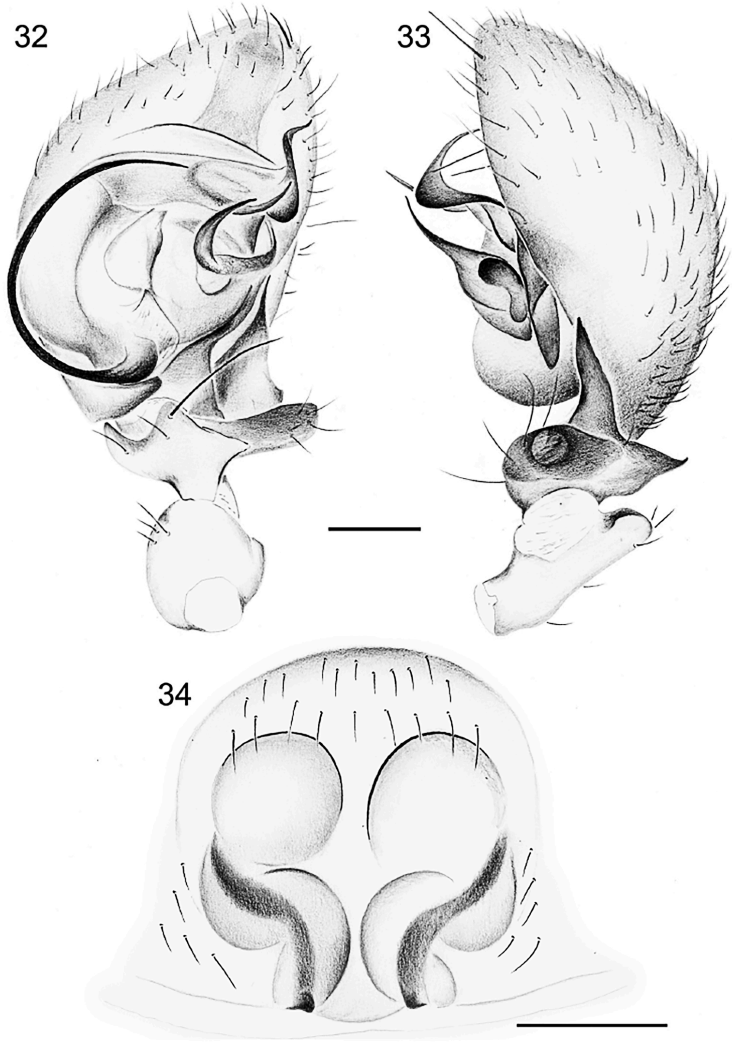
Palp. (Figs 28, 29, 32, 33, 42–45). Patella with short, rounded dorsal extension; tibia with short dorsal and retrolateral anterior extensions; remainder of palp very similar to that of *S. chawia* except the shape of the distal part of the conductor which sharply curved with rounded tip and provided with a small triangular extension; distal prong of MA broad and ridged.

Female (Paratype MRAC 241686)

Total length 2.70, carapace 1.21 long, 0.78 wide and 0.58 high. **Carapace** (Fig. 27), mouthparts and eyes as in male. **Abdomen** not modified (Figs 27, 46), anteriorly provided with granulated gland outlet (Fig. 47); dorsum

uniform dark sepia, sides paler sepia, venter pale with two oblique dark patches extending from dark sides and dark spot in front of white spinnerets.

Chilum single, 0.08 high, 0.11 wide; trapezoidal, slightly protruding in the centre, inferior margin procurved. Chelicerae promargin with two slanting teeth, the proximal one larger and retromargin with one small, sharp tooth (Fig. 41). Labium inverted U shaped (Fig. 39). Endites roughly triangular, strongly converging, distally with special asymmetric setae: anterior part bifid, the longer branch with both margins serrated, the smaller branch conical and smooth (Fig. 40).

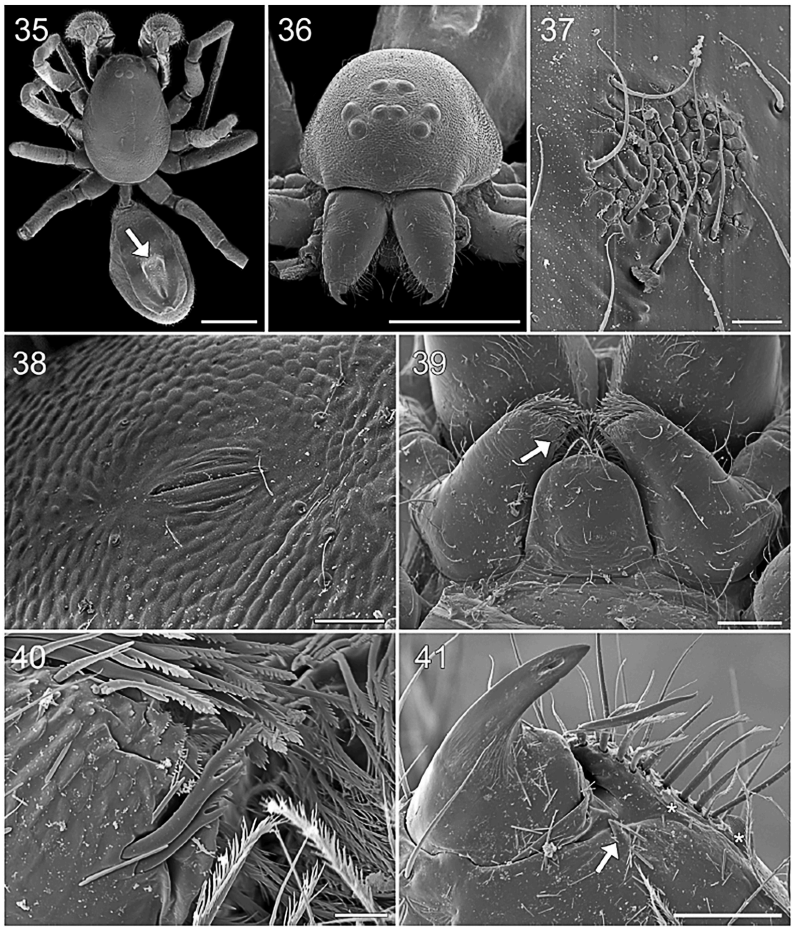


FIGURES 32–34. *Suffrica exotica* **sp. n.**, male palp and female epigyne drawings; (32) male holotype (MRAC 241686), palp, ventral view; (33) as previous, retrolateral view; (34) female paratype (MRAC 241686), epigyne, ventral view. Scale bars = 0.1 mm.

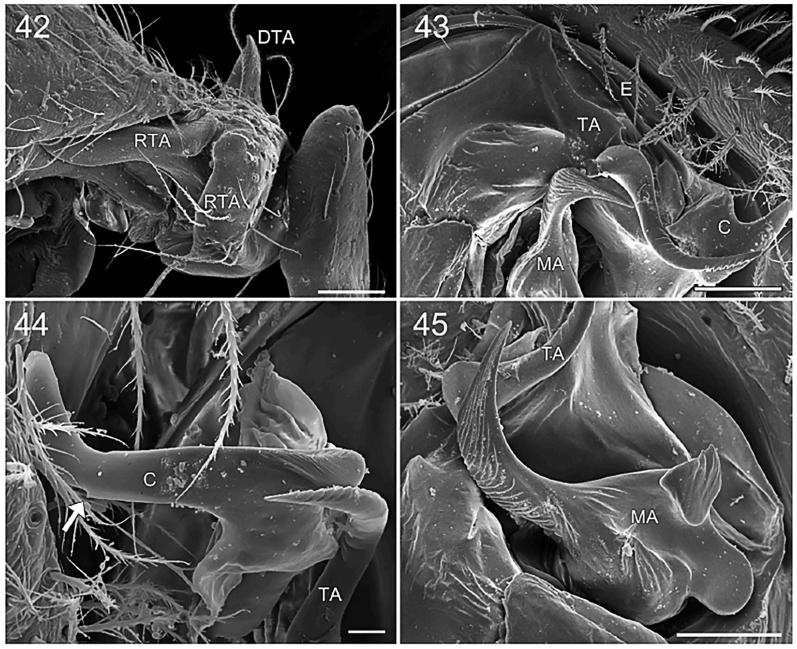
Sternum: 0.61 long, 0.54 wide.

Leg measurements:

	Fe	P	T	Mt	t	tot
I	0.75	0.30	0.57	0.54	0.45	2.61
II	0.57	0.24	0.42	0.45	0.39	2.07
III	0.48	0.24	0.42	0.54	0.33	2.01
IV	0.78	0.30	0.69	0.78	0.51	3.06



FIGURES 35–41. *Suffrica exotica* **sp. n.**, male and female paratype (MRAC 215732), SEM views; (35) male habitus, dorsal view; (36) male carapace, anterior view; (37) male, detail of the abdominal gland, dorsal view; (38) male, fovea region, dorso-lateral view; (39) female, labium and endites, ventral view, arrow points to the special asymmetrical setae on the endites; (40) female, antero-mesal part of the left endite with detailed view on the asymmetrical setae; (41) female, anterior part of chelicerae, ventral view, asterisks indicate two slanting teeth on the promarging and arrow points to the small sharp tooth on the retromargin. Scale bars (35, 36) = 0.5 mm; (38) = 50 µm; (39) = 100 µm; (37, 40) = 10 µm.



FIGURES 42–45. *Suffrica exotica* **sp. n.**, male paratype (MRAC 215732), SEM views of the palp; (42) detail of the tibial apophyses, retrolateral view; (43) detail of the tegular apophysis, ventral view; (44) detail of the conductor, anterior view, arrow indicates the small spiniform extension on the promargin of the conductor; (45) detail of the median apophysis. **C** = conductor, **E** = embolus, **MA** = median apophysis, **TA** = tegular apophysis. Scale bars (42, 43, 45) = 50 μm; (44) = 10 μm.

Palp (Fig. 48) with finely pectinated claw, turned inward over 45°.

Epigyne (Figs 30, 34, 54, 60): anterior part with two large adjacent circular areas with dark sclerotized anterior rim delimiting large funnels; posterior part with two slightly separated kidney shaped spermathecae. Vulva (Figs 31, 56, 57, 62) anteriorly with large, rounded, membranous structures (= funnels) (Fig. 58) ending in sinuous sclerotized copulation ducts, leading to poorly defined spermathecae. Funnels internally with numerous "lollipop" glands (Figs 59, 63), opening through small holes on the outside (Figs 55, 60–63).

Variation. Total length varies between 2.3 and 2.7 for males (n= 23), between 2.4 and 3.3 for females (n= 11). Carapace color varies from pale orange to dark reddish-brown with the small darker area in front of fovea more or less pronounced.

Distribution. Only known from the type locality in Mkomazi Game Reserve, Tanzania (Fig. 96).

***Suffrica gus* sp. nov.**
Figs 64–96

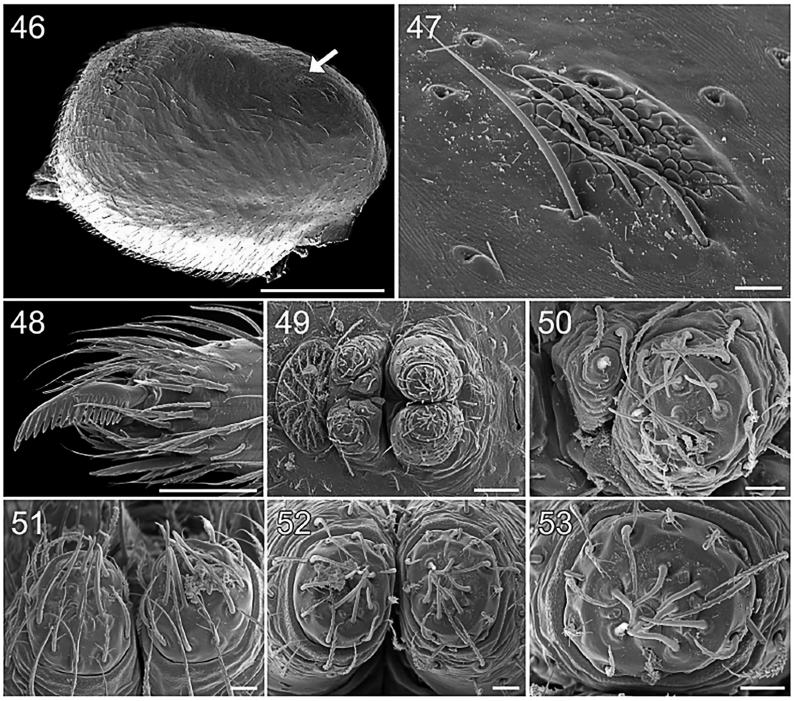
Type material. Holotype. TANZANIA: ♂: Tanga, West Usambara Mts., Mazumbai Forest, 4°49'S 38°30'E, 1400–1800m, 11–20.XI.1995, sifting litter, C. Griswold, N. Scharff & D. Ubick (ZMUC).

Paratypes. TANZANIA: 3♂ 6♀, same data as holotype; 1♂ 2♀ 6 j. : as previous (ZMUC); 1♂ 1♀ 2 j: as previous, 11–19.XI.1995, pitfall traps (ZMUC); 1♀: Tanga, East Usambara Mts., Amani, Mbomole Hill, 5°5.7'S 38°39'E, 1000m, 5–8.XI.1995, sifting litter, C. Griswold, N. Scharff & D. Ubick (CAS); 1♂: as previous, Amani, forest, 5°5.7'S 38°38'E, 950m, 27.X–9.XI.1995 (ZMUC); 1♀: Tanga, East Usambara Mts., Sangarawe Forest,

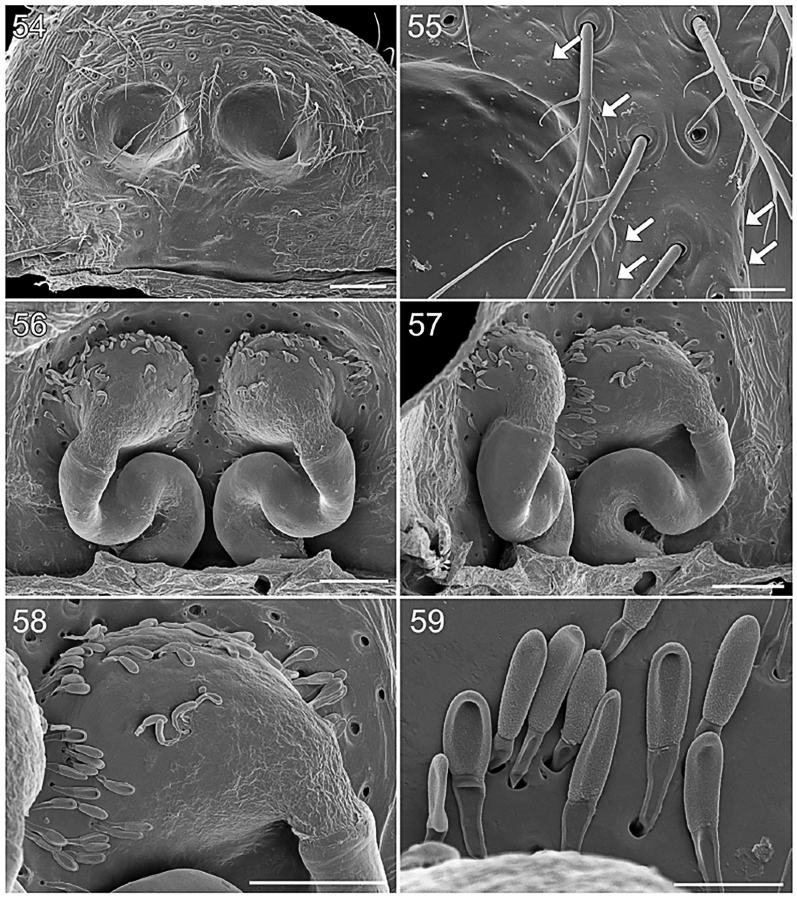
5°6.5'S 35.7'E, 990m, 5–6.XI.1995, sifting litter, C. Griswold, N. Scharff & D. Ubick (ZMUC); 2♂ 1♀: Tanga, West Usambara Mts., 4°49'S 38°30'E, 1400–1600m, 11–19.XI.1995, pitfalls, C. Griswold, N. Scharff & D. Ubick (CAS); 8♂ 2♀ 2j. : Tanga, East Usambara Mts., Amani, 5°5.7'S 38°38'E, 950m, 28.X–9.XI.1995, pitfalls, C. Griswold, N. Scharff & D. Ubick (ZMUC); 19♂ 5♀ 5j. : Tanga, East Usambara Mts., Amani, 5°5.7'S 38°38'E, 950m, 28.X–9.XI.1995, pitfalls, C. Griswold, N. Scharff & D. Ubick (CAS; 2 ♂ 2♀ kept in MRAC); 2♂ 2♀ 2j. : as previous (CAS); 1♀: Tanga, East Usambara Mts., Kwamkoro Forest Reserve, 5°10.9'S 38°35.8'E, 950m, 6.XI.1995, C. Griswold, N. Scharff & D. Ubick (ZMUC).

Diagnosis. Specimens of *S. gus* are recognized by the absence of a dark patch in front of the fovea (Figs 64, 66). The males are easily diagnosed by the row of thin spines on the conductor of the palp (Fig. 89), the thin and smooth distal prong of the MA (Fig. 87) and the abdominal modification: the central groove is shallow and delimited by whitish, narrowing and converging ridges and a small protruding pale brown scutum in front (Figs 65, 74, 75). The female differs from that of *S. exotica* by the less developed circular entrance in the frontal half of the epigyne and by the more angled copulation ducts (Figs 69, 72, 73, 90–92, 94).

Etymology. The species name is a noun in apposition derived from the first letter of the surnames of the collectors.



FIGURES 46–53. *Suffrica exotica* **sp. n.**, female paratype (MRAC 215732), SEM views; (46) abdomen, lateral, slightly dorsal view, arrow indicates the abdominal gland pores; (47) detail of the abdominal gland, dorso-lateral view; (48) detail of the right palpal claw, dorsal view; (49) overview of the spinnerets, anterior view; (50) posterior lateral spinnerets and median spinnerets, anterior view; (51) anterior lateral spinnerets, antero-lateral view; (52) as previous, anterior view; (53) as previous, detail. Scale bars (46) = 0.5 mm; (47, 50–53) = 10 µm; (48, 49) = 50 µm.

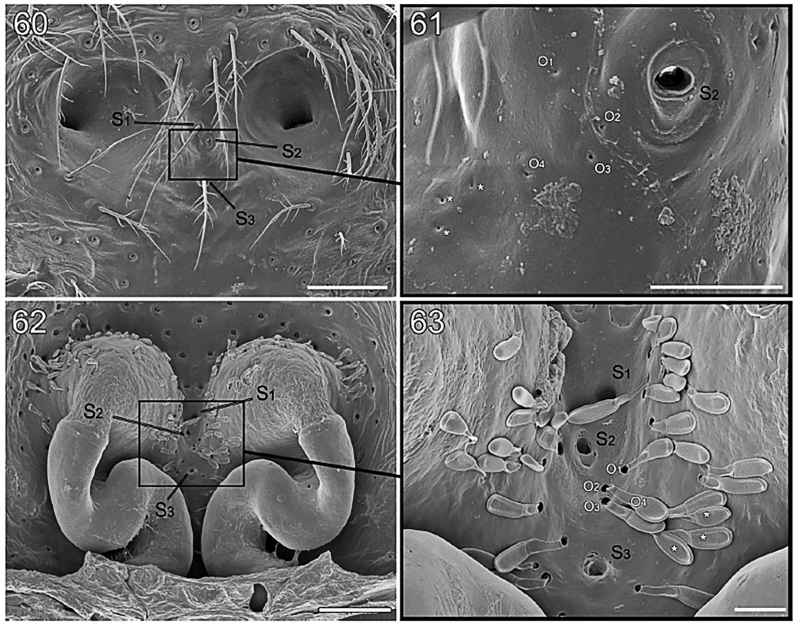


FIGURES 54–59. *Suffrica exotica* **sp. n.**, female paratype (MRAC 215732), SEM views of genitalia; (54) epigyne, ventral view; (55) as previous, detail, arrows point to some of the tiny outlets of epigynal glands; (56) vulva, dorsal view; (57) as previous, dorso-lateral view; (58) as previous, detail; (59) detail of the "lollipop" epigynal glands. Scale bars (54, 56–58) = 50 µm; (55, 59) = 10 µm.

Description. Male (Holotype). Total length 2.41, carapace 1.14 long, 0.78 wide and 0.50 high. **Carapace** (Figs 64, 74) very finely reticulated, medium brown, without dark area in front of fovea or if so, very faint; chelicerae and chilum pale brown; sternum yellow; legs yellow, femora slightly darker brownish. **Clypeus** 0.18 high. **Eyes** AME: 0.07: ALE: 0.08; PME: 0.08; PLE: 0.08; AME–AME: 0.04; AME–ALE: 0.05; PME–PME: 0.03; PME–PLE: 0.10. MOQ: width 0.16 in front, 0.18 at the back; 0.23 long.

Chilum single, 0.07 high, 0.12 wide; trapezoidal, slightly protruding in the centre, inferior margin concave. **Sternum:** 0.59 long, 0.53 wide.

Legs: spination: Fe: I d1 II d1 III d1 IV d2; T (all spines except dorsal at distal extremity): III d1 middle pl1 v2 IV d1 at 2/3 pl1 v2; Mt (all spines at distal extremity): I v(pl)1 IIv(pl)2 III dw4 IV dw4. Metatarsi with three claws. Metatarsi II and III with preening brush of short chisel-shaped setae.



FIGURES 60–63. *Suffrica exotica* **sp. n.**, female paratype (MRAC 215732), SEM views of genitalia indicating the link between the tiny pore and the "lollipop" glands; (60) epigyne, ventral view; (61) as previous, detail; (62) vulva, dorsal view; (63) as previous, detail. **S** = setae, **O** = opening. Asterisks indicate the outlets of the "lollipop" glands. Scale bars (60, 62) = 50 µm; (61, 63) = 10 µm.

Leg measurements:

	Fe	P	T	Mt	t	tot
I	0.72	0.30	0.69	0.51	0.48	2.70
II	0.63	0.27	0.42	0.42	0.42	2.16
III	0.60	0.30	0.39	0.48	0.42	2.19
IV	0.87	0.30	0.72	0.75	0.48	3.12

Abdomen (Figs 65, 74, 75): dorsum with very faint brown sclerotization front of shallow central longitudinal dorsal furrow, delimited on sides by whitish, smooth, narrowing and converging ridges and small protruding scutum in front. Anteriorly provided with brownish orange oval, glandular outlet area with granulated tegument and thin needle-like seate (Figs 65, 77); internal view shows perforated oval area, with numerous pits, larger ones corresponding with the smooth setae, smaller ones accommodating the outlets of balloon-shaped glands (Figs 79–81). Sides sepia, venter pale, somewhat darkened around pedicel and in front of white spinnerets.

Palp. (Figs 67, 68, 70, 77, 86–89). Patella with fairly long dorsal extension; tibia with short dorsal and retrolateral anterior extensions; remainder of palp very similar to those of *S. chawia* and *S. exotica* except shape of distal part of conductor strongly curved and which is provided with a row of retrolateral needle-like spines; distal prong of MA slender.

Female (Paratype CAS). Total length 2.84, carapace 1.35 long, 0.85 wide and 0.71 high. **Carapace** (Fig. 66), mouthparts and eyes as in male. **Abdomen** not modified; dorsum uniform dark sepia with numerous tiny white spots, with small pale scutum provided anteriorly with oval glandular outlet (Figs 77, 78); sides paler sepia, venter

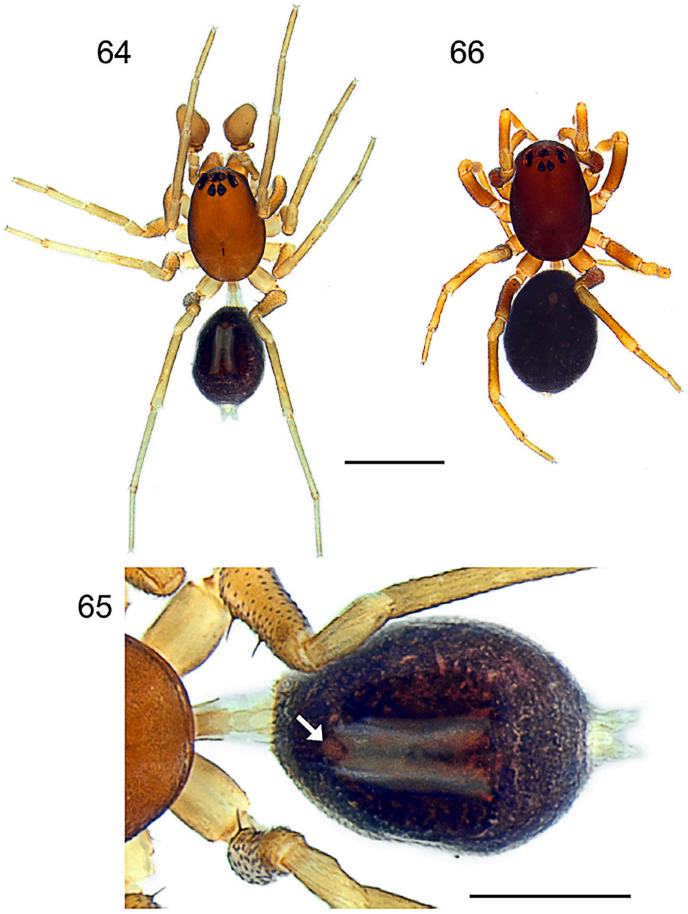
pale with two oblique dark patches extending from dark sides and dark spot in front of white spinnerets, surrounded by pale ring.

Chilum 0.07 high, 0.12 wide; trapezoidal, inferior margin straight.

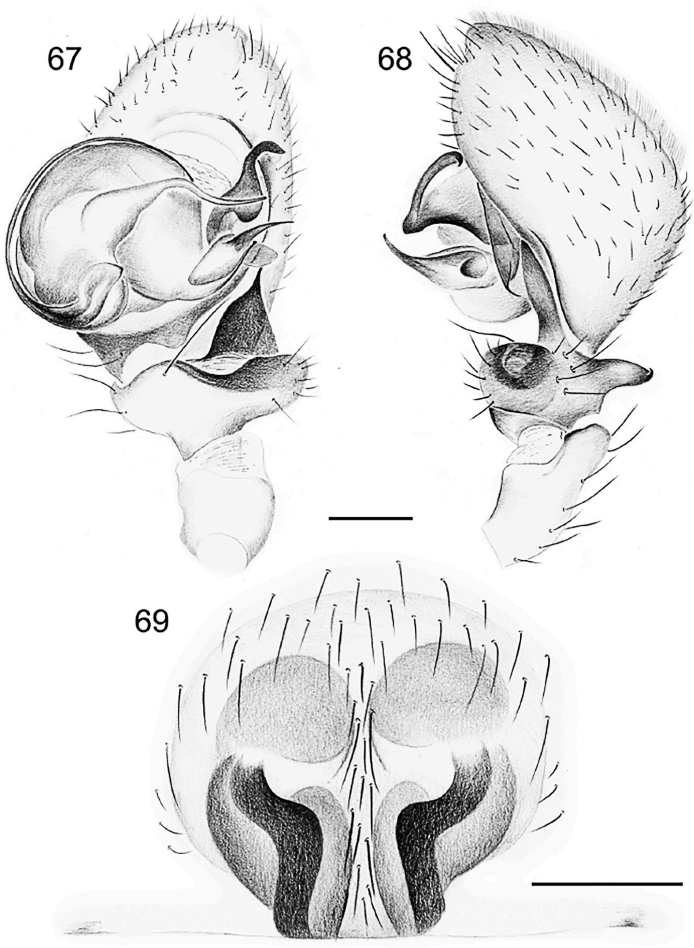
Sternum: 0.64 long, 0.57 wide.

Legs: spination as in male. **Leg measurements:**

	Fe	P	T	Mt	t	tot
I	0.69	0.30	0.63	0.51	0.45	2.58
II	0.66	0.30	0.48	0.48	0.36	2.28
III	0.63	0.30	0.45	0.36	0.39	2.13
IV	0.84	0.30	0.69	0.75	0.48	3.06



FIGURES 64–66. *Suffrica gus* **sp. n.**, male and female paratype (CAS); (64) male habitus, dorsal view; (65) as previous, detail of the abdomen, arrow points to the abdominal glandular outlet; (66) female habitus, dorsal view. Scale bar (64, 66) = 1 mm; (65) = 0,5 mm.



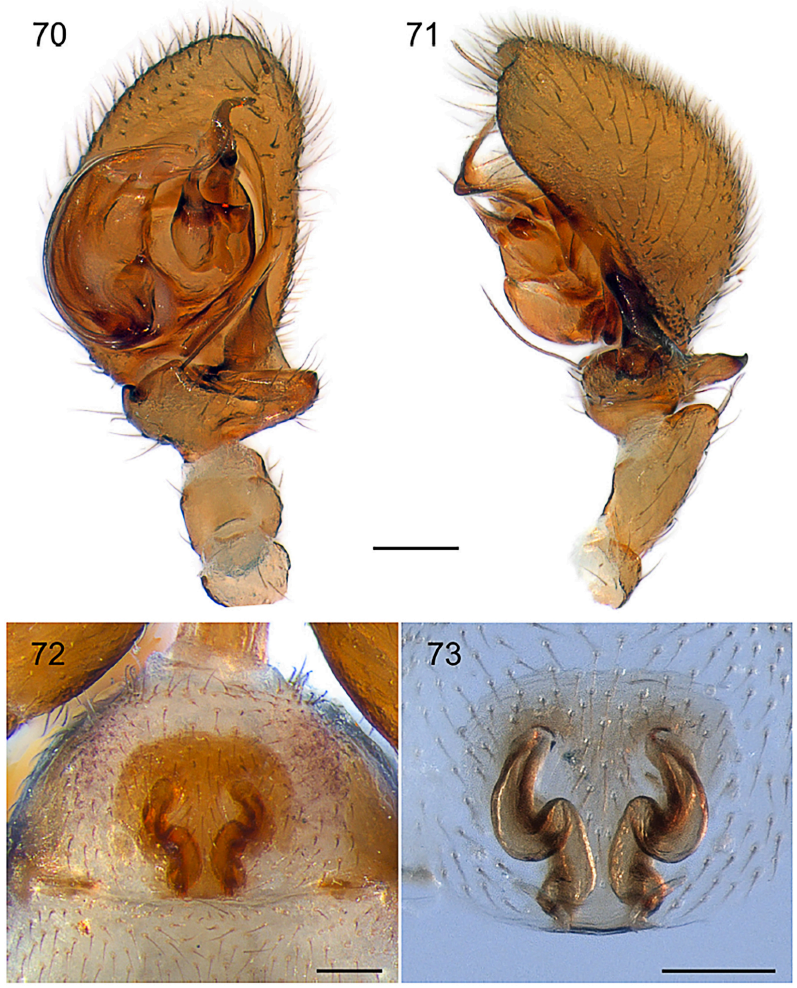
FIGURES 67–69. *Suffrica gus* **sp. n.** (CAS), male palp and female epigyne drawings; (67) male palp, ventral view; (68) as previous, retrolateral view; (69) female epigyne, ventral view. Scale bars = 0.1 mm.

Palpal tarsus with 4–5 strong prolateral spines, with finely pectinated claw (Fig. 85).

Epigyne. (Figs 69, 72, 90, 91). Provided with vase shaped medium brown pattern composed of entrance ducts and spermathecae seen in transparency. Vulva anteriorly with two membranous tube-shaped structures connected to the sinuous copulation ducts, leading to poorly defined elongated spermathecae (Figs 73, 92–94). Anterior membranous part internally with "lollipop" glands at its vicinity (Fig. 95) as in *S. exotica* but less numerous.

Variation. Total length varies between 1.9 and 2.5 for males (n= 24), between 2.3 and 2.7 for females (n= 19). The longitudinal dorsal ridges on the male abdomen may vary in width.

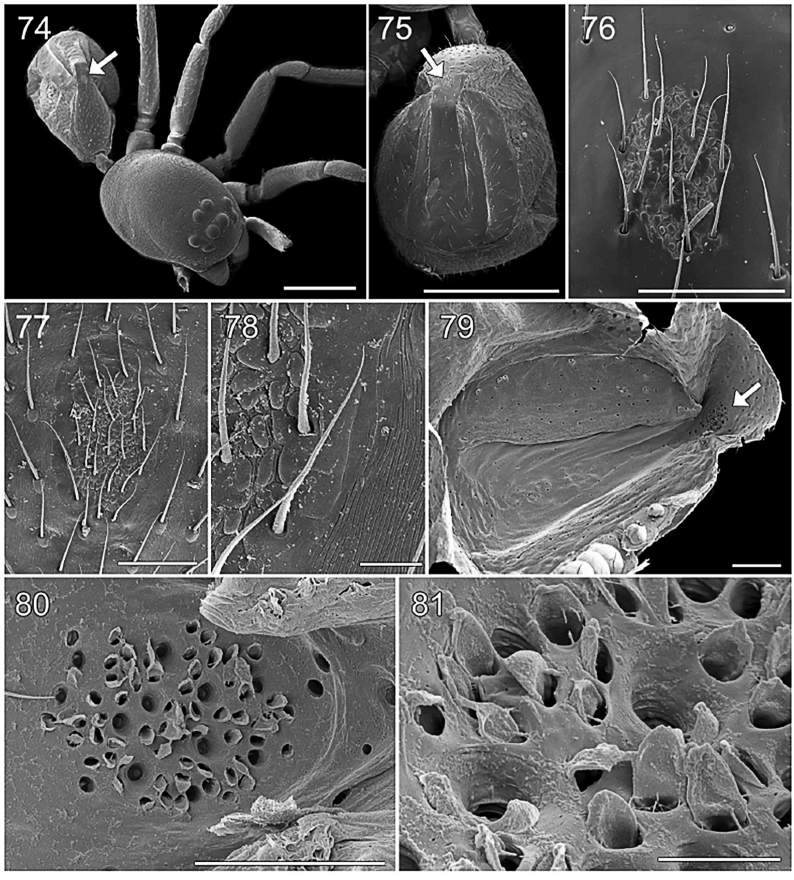
Distribution. Known from several localities in the Usambara Mts. in Tanzania (Fig. 96).



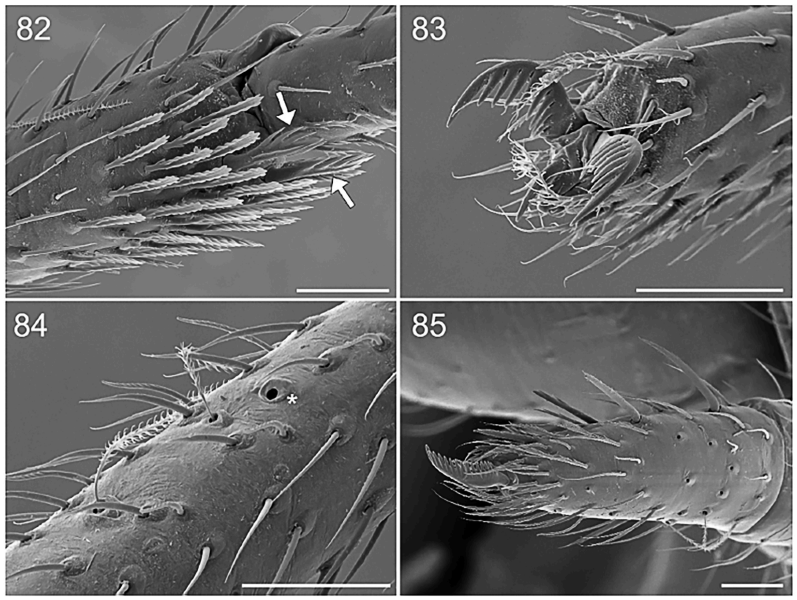
FIGURES 70–73. *Suffrica gus* **sp. n.** (CAS), male palp and female epigyne; (70) male palp, ventral view; (71) as previous, retrolateral view; (72) female epigyne, ventral view; (73) female vulva after digestion, dorsal view. Scale bars = 0.1 mm.

Discussion. The discovery of several species of a genus close to *Suffasia* may come as a surprise since the latter genus is widespread in Asia but has not yet been found in Africa. However, the localities where these species have been found, boast a particularly high biodiversity. The Eastern Arc Mountains are among the most diverse African regions (Griswold 1991; Scharff 1993; Jocqué *et al.* 2013) and are famous for a number of very remarkable organisms often with unclear affinities, e.g. the damselfly *Amanipodagrion gilliesi* Pinhey, 1962 (Dijkstra & Clausnitzer 2014) and the spiders *Arctenus taitensis* Polotow & Jocqué, 2014 (Polotow & Jocqué 2014) and *Ulugurella longimana* Jocqué & Scharff, 1986 (Jocqué & Scharff 1986). The adjacent Mkomazi Game Reserve is the area with the highest number of species of Zodariidae in the world (Haddad & Russell-Smith 2010; Russell-

Smith & Jocqué, in press). Nevertheless, the distance between the core distribution of *Suffasia* and its relatives (e.g. *Malayazodarion* Ono & Hashim, 2008) in southwest Asia and that of *Suffrica* remains remarkable. There is, however, at least one other taxon with a similar distribution: a phasianid bird from Tanzania that has Indo-Malayan affinities (see Dinesen *et al.* 1994). These authors argue that opportunities for interchange of forest biota between tropical Africa and the Orient may well have existed in the mid-Miocene, before desertification and rifting of the Red Sea isolated the two regions. This implies that the Eastern Arc is an example of a mountain refugium as explained in Jocqué *et al.* (2013). The occurrence of *S. chawia* on only one of the Taita Hills, the Chawia Forest, is another indication that this is a relic distribution. The other forests in that chain of weathered old mountains were very thoroughly sampled (see Warui & Jocqué 2002; Polotow & Jocqué 2014) but do apparently not harbor this species.



FIGURES 74–81. *Suffrica gus* **sp. n.**, SEM view of male and female (CAS); (74) male habitus, antero-dorsal view, arrows points to the abdominal glandular outlet; (75) male abdomen, dorsal view, arrows points to the abdominal glandular outlet; (76) male detail of the glandular outlet, dorsal view; (77) abdominal glandular outlet of the female, dorsal view; (78) as previous, detail; (79) male, inner view of the abdomen dorsum, arrow indicates the abdominal glandular outlet; (80) as previous, inner view of the glandular outlet; (81) as previous, detail, slightly oblique view. Scale bars (74, 75) = 0.5 mm; (76, 77, 80) = 50 µm; (78, 81) = 50 µm; (79) = 100 µm.



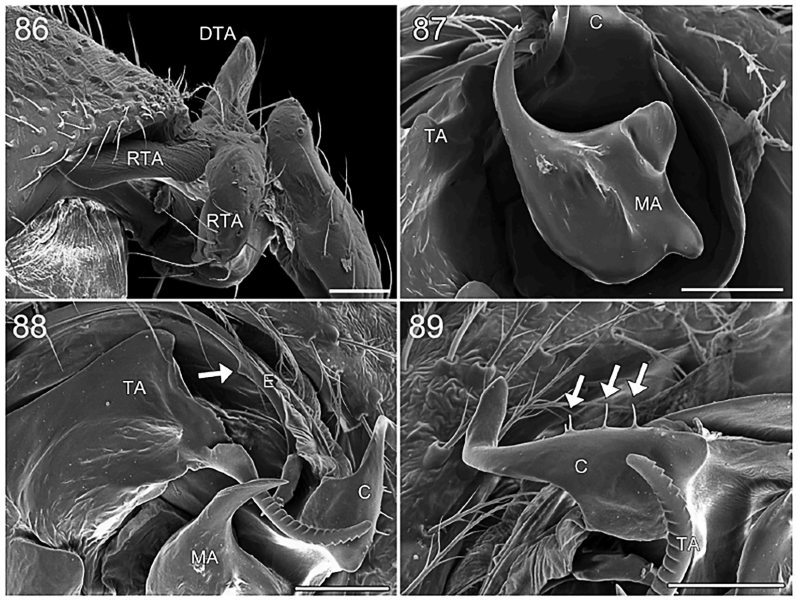
FIGURES 82–85. *Suffrica gus* **sp. n.**, SEM views of female (CAS). (82) distal part of metatarsus of leg II with detail on the chisel shaped setae, ventro-prolateral view, arrows point to the terminal ramified spines; (83) tarsal claw of leg III, antero-dorsal view; (84) proximal part of tarsus of leg I, dorsal, slightly oblique view, asterisk indicates the tarsal organ; (85) left palpal tarsus, dorsal view. Scale bars = 50 µm.

Abdominal and epigynal glands. Spiders possess a wide variety of exocrine glands but most studies have focused on the silk and venom glands (e.g. Foelix 2011). However, whereas the role of these glands is quite obvious, the role of the secretions produced by other glands is not always clear. These secretions may be involved in sexual interactions including plugging of the epigyne, defensive behavior, predation and intraspecific communication (e.g. Eberhard 1980; Lopez 1998). On the ventral side of the abdomen, at the level of the epigastric furrow, epigastric glands have been found in both male and female spiders belonging to various families (Lopez 1974, 1984; Kovoor *et al.* 1981). Their role is still uncertain and they appear to have a distinct function in each sex (Pekár & Šobotník 2007).

So far, no glands have been reported from the dorsum of the abdomen. In *Suffrica*, both male and female possess a glandular outlet on the dorsal side of the abdomen. This glandular outlet is visible as an oval area situated anterior to the mid-dorsum (Figs 6, 35, 46, 65, 74, 75) and has a granulate surface provided with small, smooth setae and a few tiny pores which are not always visible (Figs 8, 9, 37, 47, 76–78). Internally, the glandular outlet looks like a perforated area, with pits of different sizes: the larger pits correspond to the base of the setae and the smaller ones accommodate the outlet of a flat, oval gland (Figs 79–81). The flat appearance is doubtlessly the result of the digestion and drying processes during which the glands collapsed. They are probably either cylindrical or ampullate. A similar effect could also explain the flat appearance of the "lollipop" glands in the epigyne.

The epigynal glands appear to be organized in two parts: the proximal part is balloon-shaped, and the distal part tube-shaped or pedicel-like, entering in a large pit in the tegument and leading to a tiny pore in the outer surface. The size difference of the pores in the outer and inner side may be surprising. In Foelix (2010) (fig. 2.33C p.46), one can see a section of a dermal gland and the important constriction of the canal at the level of the outer cuticle. Furthermore, it could be traced for the "lollipop" epigynal gland (see Figs 60–63).

The role of neither the dorsal abdominal glands nor the "lollipop" epigynal glands are known, and histological studies are needed to classify them.



FIGURES 86–89. *Suffrica gus* **sp. n.** (CAS), SEM views of the male palp; (86) detail of the tibial apophyses, retrolateral view; (87) detail of the median apophysis, ventral view; (88) detail of the tegular apophysis, ventral view, arrow points to the small triangular extension on the embolus; (89) detail of the conductor, anterior view, arrows indicate the thin, needle-like extensions on the retromargin of the conductor. **C** = conductor, **E** = embolus, **MA** = median apophysis, **TA** = tegular apophysis. Scale bars = 50 µm.

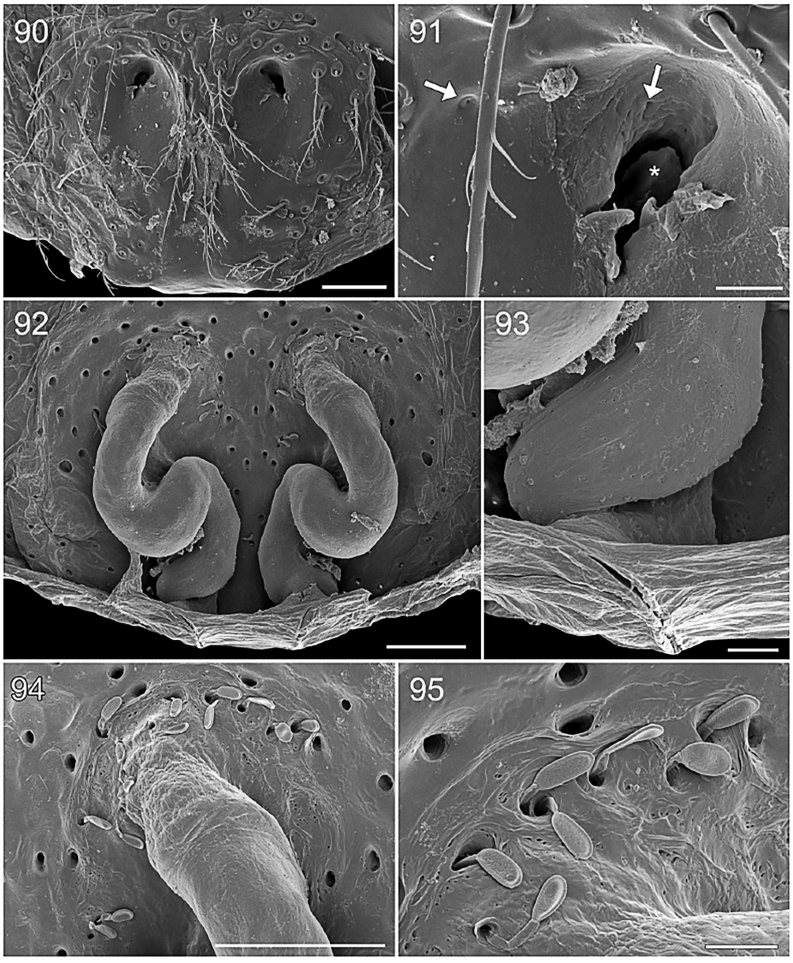
Femoral Organ. The first observation of a femoral organ in Zodariidae was made by Tucker (1920) on several *Diores* species from South Africa. He mentioned a "distinct patch of short spiniform bristles" on the distal part of legs I–III, "giving the appearance of a sense organ". The femoral organ was later found in different genera by Jocqué & Billen (1987) and Jocqué (1988). Their studies showed a remarkable range of variation in the structure of the gland outlet and of the bristles associated with it. A detailed study (Pekár & Šobotník 2007) of the femoral gland itself in the genus *Zodarion* clearly demonstrated its role as an exocrine gland. Although it has been suggested that the gland produces a volatile compound, the composition of the secretion is unknown and the exact role of the femoral organs remains obscure. However, as most of the Zodariinae with these glands are specialised consumers of ants or termites, it is assumed that they may be involved in the predation of these insects (Jocqué & Dippenaar-Schoeman 1992; Pekár 2004; Pekár *et al.* 2008). The gland might produce a secretion imitating the prey ant's pheromone rendering the attack less hazardous (Jocqué 1988) or a product that could prevent intraspecific attacks or cannibalism.

The femoral organ may be qualified as "simple" when it consists of a few smooth setae in a shallow depression provided with pores (i.e. *Suffasia*, *Suffrica* and *Asceua* (pers. obs.)) or may be considered "complicated" when provided with barbed setae (i.e. *Zodarion*, *Diores*, …). In rare cases it is encapsulated in a deep alveolus (e.g. *Heradida*). Jocqué (1991) even postulated a hierarchical evolution of these femoral organs from the simple form towards the more complicated one. However, this hypothesis should be tested in a cladistic analysis. A detailed study of the morphology and distribution of the femoral organ in the subfamily Zodariinae is under way.

Until now it was thought that in most Zodariinae, only a single organ was present on each of the femora on which the gland is found (e.g. Pekár & Šobotník 2007). Here we clearly show that in *Suffrica* the gland is double and occurs on the pro- and retrolateral side of the distal part of the femora. A scan of other genera reveals that a similar set-up with a double gland is also present in *Asceua*, *Suffasia* and some undescribed species from

Madagascar. It is worth to recall that in Jocqué (1991), *Asceua* was placed in the subfamily Storeninae because it has the chisel-shaped setae whereas *Suffasia* was part of the Zodariinae as it has the femoral organ. Actually, both these genera are characterized by the presence of preening brushes with chisel-shaped setae (characteristic for the Storeninae) and two femoral organs present on each femur. As a consequence, Jocqué (1992) fused the two subfamilies into the Zodariinae.

However, the external structure of the dual femoral organs appears different from the unique, barbed-setae ones in the other Zodariinae (sensu Jocqué 1991). Pekár & Šobotník (2007) also noted major differences in the internal structure of the gland between *Suffasia* (studied in Jocqué & Billen 1987) and *Zodarion*. This may provide an argument for the resurrection of the subfamily Storeninae, that will be tested in future analyses.



FIGURES 90–95. *Suffrica gus* **sp. n.**, SEM views of female genitalia; (90) epigyne, ventral view; (91) as previous, detail of the opening, star indicates a piece of plug and arrows point to some tiny pores; (92) vulva, dorsal view; (93) as previous, detail of the posterior part of elongate spermathecae; (94) as previous, detail of entrance ducts; (95) detail of the "lollipop" epigynal glands. Scale bars (90, 92, 94) = 50 µm; (91, 93, 95) = 10 µm.

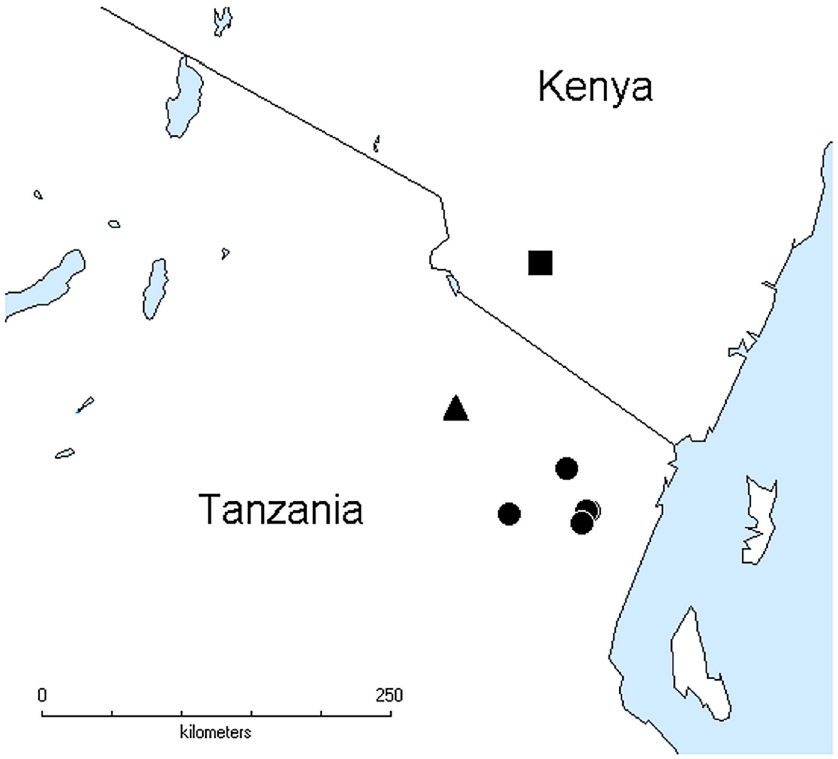


FIGURE 96. Distribution of *Suffrica* species: (■) *S. chawia*, (▲) *S. exotica*, (●) *S. gus*.

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SUB-CHAPTER IIIB

– THE NEW GENUS SUFFASCAR *ENDEMIC TO MADAGASCAR*

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A new ant-eating spider genus *Suffascar* (Araneae : Zodariidae) endemic to Madagascar: a considerable extension of the dual femoral organ clade

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Abstract. The new zodariid genus *Suffascar*, gen. nov. is described from Madagascar. It is apparently endemic to the island, common and speciose. Twelve new species were discovered and are here described: *Suffascar albolineatus*, sp. nov., *S. fianara*, sp. nov., *S. fisheri*, sp. nov., *S. fitzpatrickae*, sp. nov., *S. gigas*, sp. nov., *S. griswoldi*, sp. nov., *S. macromma*, sp. nov., *S. micromma*, sp. nov., *S. nonus*, sp. nov., *S. scutatus*, sp. nov., *S. sufficiens*, sp. nov. and *S. tofti*, sp. nov. It is well known that Zodariidae with femoral organs are specialised consumers of ants or termites, although the exact role of these glands still remains obscure. *Suffascar* is part of the 'dual femoral organ clade' (DF), which also includes *Asceua* Thorell, 1887, *Suffasia* Jocqué, 1991, and *Suffrica* Henrard & Jocqué, 2015. Using a morphology-based phylogenetic analysis, we test whether zodariids sharing the dual femoral organ are part of the same group as the 'single femoral organ clade' (SF) or form a separate monophyletic group. It appears that SF and DF constitute clearly monophyletic entities with a sister-group relation. These groups may be considered as distinct subfamilies and, together, they may turn out to be sister to the Storeninae (which then could be re-established). An analysis that focuses on these questions is underway.

http://zoobank.org/urn:lsid:zoobank.org:pub:281E1357-FAEE-4300-B1BB-F0D43E724E91

Additional keywords: chisel-shaped setae, cladistic analysis, femoral gland, *Suffrica*, Zodariinae.

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Introduction

Many zodariid spiders feed on ants, although some are generalist predators and may also eat other invertebrates (Simon 1910; Ramírez 1995; Rössl and Henschel 1999). *Zodarion* Walckenaer, 1826 species have even been found to mimic (anatomically and behaviourally) ants when preying on them (Pekár and Kŕál 2002; Pekár *et al.* 2008). This behaviour gives the group their vernacular name of 'ant-eating spiders'. Many zodariids also possess glands, known as 'femoral organs', on the femora of legs. Femoral organs were first observed by Tucker (1920) on some *Diores* Simon, 1893 species from South Africa. He described them as 'distal patches of bristles on outer surface of femora' (p. 472) and also mentioned that 'a paler ring surrounds the group of short bristles giving the appearance of a sense organ' (p. 472). Many other zodariid taxa have since been found to possess femoral organs, sometimes with varying morphology, such as the shape of the associated bristles (e. g. Jocqué and Billen 1987; Jocqué 1988, 1992, 2011; Szüts and Jocqué 2001; Jocqué and Churchill 2005; Cushing 2012; Jocqué and Henrard 2015*a*; Russell-Smith and Jocqué 2015). A detailed study of the femoral gland in the genus *Zodarion* clearly demonstrated that it has the structure of an exocrine gland (Pekár and Šobotník 2007). Although it has been suggested that the gland produces a volatile compound, the composition of the secretion and the exact role of the femoral organs remain unknown to date.

Zodariidae with femoral glands are specialised, sometimes exclusive, consumers of ants or termites (e.g. Jocqué and Dippenaar-Schoeman 1992; Pekár 2004; Pekár and Toft 2009; Monzó *et al.* 2013; Pekár *et al.* 2014; Cárdenas *et al.* 2014; Komatsu 2016). It is therefore assumed that the femoral gland may be involved in the predation of these insects. The gland might produce a secretion imitating the prey ant's pheromone and rendering the attack less hazardous (Jocqué 1988) or a product that could prevent intraspecific attacks or cannibalism (Henrard and Jocqué 2015).

Zodariids with a single femoral organ on each leg form a well supported group, the Zodariinae *sensu* Jocqué (1991). Whereas the femoral organ was thought to be present uniquely on the prolateral face of the distal part of the femora, it has recently been found on the prolateral and retrolateral faces of all legs in the

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genera *Asceua* Thorell, 1887, *Suffasia* Jocqué, 1991 and *Suffrica* Henrard & Jocqué, 2015 (Henrard and Jocqué 2015). This group was then dubbed the 'dual femoral organ' clade. With the discovery of species with paired femoral glands, it is now questionable whether zodariids sharing the dual femoral organ are part of the same group as the species with a single femoral organ, or form a distinct monophyletic group. The femoral organ was actually overlooked in *Asceua* by Jocqué (1991) and was placed in the subfamily 'Storeninae'. Indeed, species of *Asceua* have the preening brushes with chisel-shaped setae, a purported synapomorphy for this subfamily (Jocqué 1991). *Suffasia* was considered part of Zodariinae because its species have femoral organs. However, *Suffasia* was later discovered to have both preening brushes with chisel-shaped setae and femoral organs on each femur. As a consequence, Jocqué (1992) fused Storeninae into the Zodariinae.

The present paper deals with a new genus that clearly belongs to the dual femoral gland clade. It is apparently restricted to Madagascar, where it appears to be very common and speciose. Twelve new species were found in museum collections and are here described. To place it in a phylogenetic context and to test the monophyly of the 'dual femoral organ clade', a cladistic analysis based on morphological characters was performed. It includes some taxa from the 'single femoral organ clade' and some other taxa without femoral organs but possessing chisel-shaped setae (see Jocqué 1991, 1992).

Material and methods

Measurements and coloured photographs of the habitus, details of mouthparts or legs, detached male palps and female genitalia were taken with a Leica MZ16 using the Leica Application Suite (LAS) automontage software (ver. 3.8; Leica, https://leica-camera.com). The female genitalia were dissected and digested using half a tablet of Total Care Enzima product (protein removal system originally for cleaning contact lenses and containing subtilisin A-0,4 mg per tablet; Abbott Medical Optics, Santa Ana, CA) in a few millilitres of distilled water for several hours or overnight. The digested genitalia was then immersed in 75% ethanol or dried for scanning electron microscopy (SEM) observation. Details of the female genitalia and male palps were drawn with a WILD M10 stereomicroscope (Leica). For scanning electron micrographs, dissected body parts and genitals were first immersed in few millilitres of acetone (24 h), then dried by a rapid evaporation of acetone on a heated plate (set at ±60°C). Dried parts were then gold coated and examined and photographed with a JEOL 6480 LV scanning electron microscope. Some legs and body parts were processed for SEM after use in a DNA extraction protocol (see Paquin and Vink 2009; Henrard and Jocqué 2015). Illustrations were assembled and edited in Adobe Photoshop CS5 (adjusted for white balance and colour contrast; www.adobe.com). Types are deposited in the Royal Museum for Central Africa, Tervuren, Belgium (MRAC) and California Academy of Sciences, San Francisco, USA (CAS). All measurements are in mm (unless otherwise noted).

Samples labelled 'DNA Z' such as 'DNA Z100', 'DNA Z302' or 'DNA Z304' are samples that were chosen for DNA extraction and molecular studies (unpubl. data).

Distribution maps were created with QGIS, a free and open source geographic information system (http://www.qgis.org/), and edited with Adobe Photoshop CS5.

Cladistic analysis

The parsimony analysis was based on 21 taxa and 78 characters (see Table 1 for matrix). The distribution of characters includes: carapace and sternum (13), eyes (7), mouthparts (11), legs (18), female palp (7), male palp (10) and abdomen and spinnerets (12) (see Table 2). Based on preliminary results (unpubl. data), *Hermippus* Simon, 1893 was chosen as the outgroup and some representatives with chisel-shaped setae but no femoral gland (i.e. *Mallinella* Strand, 1906, *Heradion* Dankittipakul & Jocqué, 2004 and *Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012) and some taxa of 'the single femoral organ clade' that were available for the study were also included in the analysis (Appendix 1).

The analysis was conducted in TNT 1.1 (Goloboff *et al.* 2003, 2008) and NONA 2.0 (Goloboff 1993) (set to 512 Mb), with maximum trees in memory and using 'implicit enumeration' tree search to find parsimonious trees. As measures of robustness, we calculated bootstraps (output results as absolute frequencies) and Bremer (absolute) supports using 'implicit enumeration' tree search. The 'ratchet' in Winclada 1.00.08 (Nixon 1999–2002) gave the same tree topology and was used with default settings to calculate the consistency index (CI) and the retention index (RI). The same program was used to illustrate the character state changes (unambiguous changes only) and the support values were depicted on this (unique) parsimonious tree (Fig. 1).

Institutional repositories

CAS	California Academy of Science, San Francisco, USA
CASENT	California Academy of Science, Entomology (Unique specimen codes of the entomology collection of the CAS)
MHNG	Muséum d'histoire naturelle de Genève, Switzerland
MRAC	Musée Royal de l'Afrique Centrale, Tervuren, Belgium
RBINS	Royal Belgian Institute of Natural Sciences, Bruxelles, Belgium
SMF	Senckenberg Museum, Frankfurt, Germany

Abbreviations

ALE, Anterior lateral eyes; AME, anterior median eyes; asl, above sea level; DTA, dorsal tibial apophysis; L, carapace length; PLE, posterior lateral eyes; PME, posterior median eyes; PMS, posterior median spinnerets; P.N., National Park; PLS, posterior lateral spinnerets; RTA, retrolateral tibial apophysis; SEM, scanning electron microscopy; W, carapace width; WSC, World Spider Catalog.

Results

Phylogenetics

The analysis conducted in TNT using 'implicit enumeration' tree search resulted in one unique parsimonious tree with a length of 150 steps. The 'ratchet' method in Winclada provided the same result with CI = 79 and RI = 91, and the same program was used to show the character state changes (unambiguous

Table 1. Matrix of characters used in the cladistic analysis of the Zodariidae
Characters and state are listed in Table 2. '?' denotes unknown or inapplicable characters

Taxa	Characters								
	0000000001 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6666666667 1234567890	77777777 12345678
Hermippus loricatus	0000000000	0000000?0	0000000000	000000?000	0000000000	0000000000	0000000000	00000000
Mallinella vokrensis	0010100001	1000101?0	0000010000	000000?000	0000000000	0000000001	0000000000	01010000
Heliconilla globularis	0000000001	1000101?0	0100010000	000000?000	0000000010	0000??0001	0000000000	01000000
Heradion paradiseum	0010100001	1000101?0	0100010000	000000?0?0	0010000010	0000??0001	0000000000	01000000
Suffascar albolineatus	0000101010	2011001110	1100001000	0022220010	1111010000	0110000000	0110111111	10001001
Suffascar fianara	0000101010	2011001110	1100001000	0022220010	1111010000	0110000000	0110111110	10001001
Asceua lejeunei	0000100010	1000001120	1100100000	0022220011	1111000000	0010000000	0110001110	01111101
Asceua dispar	0000100010	1000001120	1100100000	0022220011	1111000000	0010000000	0110001110	01111101
Asceua gruezoi	0000100010	1000001120	1100100000	0022220011	1111000000	0010000000	0110001110	01111101
Suffrica exotica	0000100011	1000001130	0000100000	0022220010	1111010100	0010100000	1110011110	00101001
Suffrica gus	0000100011	1000001130	0000100000	0022220010	1111010100	0010100000	1110011110	00101001
Suffasia tumegaster	0010100110	0000101120	1110100000	0022220011	1111000000	0010110000	0110001110	01101001
Suffasia kanchenjunga	0010100110	0000101120	1110100000	0022220011	1111000000	0010110000	0110001110	01101001
Acanthinozodium sericeum	1011000012	2111000?1	??11010110	1111111111	1110100001	1011000002	0111111101	10000000
Zodarion nitidum	1011000112	2111000?1	??11010121	1111111111	2110100001	1111010002	0111111100	00100000
Tropizodium siam	1011000112	2111000?1	??11010120	1101111111	2111100000	1111000002	0111111101	10101010
Palaestina expolita	2101011010	200100?0?1	??11010011	1111111111	2111100100	1111010102	0111111101	10101010
Trygetus sexoculatus	210101?01?	2?10001010?1	??11010011	1111111111	2110100100	1111010102	0111111100	00101010
Akyttara homunculus	2101010012	2011011010?1	??11010111	1111001111	2110101100	1111011112	0111111100	00101010
Heradida speculigera	2101010010	2001011010?1	??11010111	1111001111	2110101100	1111011112	0011111100	00101010
Diores poweri	1011000010	2011000?1	??11010010	1111101111	0110100000	1111000000	0011111100	01001010

changes only) on this tree (Fig. 1). Bootstrap values (Bp) and Bremer supports (Br) were calculated in TNT, both with 'implicit enumeration'. With 'suboptimal' set at 11 steps, Br was calculated from 69 566 suboptimal trees found. All values were fixed and stable excepted for the node of the single femoral organ clade (SF). For 'suboptimal' set at 12 steps and above, the number of suboptimal trees exceeded the tree memory capacity (overflowed when >99 999). Then, the Br for this node was fixed when the suboptimal value of 14 steps was reached, whereas the lower values varied slightly. Another calculation using the 'ratchet' gave similar results.

The results from the analysis (Fig. 1) show that the taxa studied here and belonging to the SF clade form a strongly supported monophyletic group (support values Bp/Br: 100/14). This SF clade is defined, after the cladistic analysis, by the following derived characters: cephalic profile flat or slightly domed (character 1 – states 1, 2); carapace pear-shaped with cervical groove conspicuous (4–1); absence of a chilum (20–1); cheliceral lamina with toothed anteromesal cusp (24–1); chelicerae basally to distally fused (29–1, 2); flattened inner face of the chelicerae (31–1); absence of chisel-shaped setae on metatarsi (32–1); a poorly developed tibial process (38–1); presence of a patellar crack (45–1); female palpal claw turned inward more than 45° (51–1); female (and male) palp with a patch of chemosensitive hairs (54–1); absence of epiandrum in the male (64–1); and modified apico-prolateral setae on the male (and female) palp (77–1).

The dual femoral organ clade (DF) has a lower support value (51/1) and is defined by three derived characters: endites provided with mesoapical modified setae (18–1); presence of a dual femoral organ (36–2); and cymbium with rounded apex (78–1). The clade also has four homoplasies.

Together, the SF and DF clades form a strongly supported monophyletic clade (99/9) defined by numerous derived characters: AME dark (9–1); hinged setae absent (39–1, 63–1); spination and hair cover on anterior leg pairs similar to that on hind legs (42–1); female palpal tarsus with very few prolateral spines (52–1, reversed in *Acanthinozodium* Denis, 1966, *Suffrica*, *Suffasia* and *Asceua*: 52–0); female palpal tarsus with reduced ventro-retrolateral spination (53–1); PMS absent in male (66–1, reversed in *Suffasia* and *Asceua*: 66–0); PMS short in female (67–1); absence of large cylindrical gland spigots on PLS and PMS of female (68–1); absence or very few prolateral spines on male cymbium (75–1).

The monophyletic clade including *Heliconilla*, *Mallinella* and *Heradion* – characterised by the presence of spines in front of the tracheal spiracle (60–1) – received good support (72/2).

Discussion

Phylogenetics

Several characters were not shown on the cladogram (Fig. 1) despite their exclusivity to a given group. For these characters, there are several possible solutions for the appearance of a state (considering fast or slow optimisation in Winclada) so the state change cannot be inferred unambiguously. For instance, this is the case for characters linked to the presence of the femoral organ on legs (characters 33 to 37), which represent important features for defining the SF and DF clades. Only the presence of the femoral organ on leg IV (36–2) showed no ambiguity in the DF clade. Because *Diores* has no femoral organ on femur IV, which is the plesiomorphic state for this character (36–0), the analysis suggests that the genus is basal to the SF clade. Also of note is that the presence of the femoral organ on legs other than leg IV

Table 2. List and description of characters and character states used for the cladistics analysis of the Zodariidae
ALE, Anterior lateral eyes; AME, anterior median eyes; DTA, dorsolateral tibial apophysis; PLE, posterior lateral eyes; PME, posterior median eyes; PMS, posterior median spinnerets; PLS, posterior lateral spinnerets; RTA, retrolateral tibial apophysis

Character	States	Notes
1. Carapace profile	(0) Strongly domed (ratio height/length >0.3) (Figs 5*D*, *C*, 12*G*, 22*C*, *D*); (1) cephalic area flat, thoracic area strongly sloping (Jocqué and Henrard 2015*a*, fig. 8D); (2) cephalic area slightly domed, thoracic area lower (Jocqué 1991, figs 53, 290)	The shape of the carapace is strongly related with the life style. Burrowing species do apparently need a higher carapace than free-living ones. Zodariids that build so called 'igloo-shaped retreats' use less effort than those that remove sand and debris to construct a burrow. Although a 'flat' carapace usually has its highest point near the fovea, just as a domed one, it is considered flat when its length exceeds three times its height.
2. Highest point of carapace in lateral view	(0) Highest point around middle (Figs 5*D*, 12*G*); (1) highest point clearly in anterior part	
3. Carapace surface	(0) finely reticulated or rugose (Figs 5*A*, *C*, *D*, 15*B*, *G*); (1) smooth	The texture of the tegument varies from almost textureless to deep granulations as in *Heliconilla globularis*. When the cephalic area is smooth whereas the surrounding sides are granulose, it is coded as (0).
4. Shape of carapace in dorsal view	(0) Oval or ovoid, cervical grooves absent or faint (Fig. 12*A*, *B*); (1) pear-shaped, cervical grooves conspicuous (Jocqué and Henrard 2015*a*, figs 1A, B)	
5. Carapace, hair cover	(0) Present; (1) hairless or very few tiny setae	
6. Carapace, fovea	(0) Clearly visible, slit like; (1) absent or faint (Jocqué 1987, figs 9, 11)	
7. Posterior eye row as seen from above	(0) Clearly procurved (Henrard and Jocqué 2015, figs 25, 35); (1) straight or slightly curved (Figs 5*A*, 12*A*)	
8. Anterior eye row as seen from front	(0) Clearly curved (Figs 5*C*, 15*C*); (1) straight or slightly curved	
9. Eye colour	(0) All eyes pale; (1) AME dark (Fig. 15*D*; Jocqué and Henrard 2015*a*, figs 1A, B)	
10. Distance between PME	(0) Between 1 and 2 × their diameter apart; (1) between 1 and 2 × the diameter of the smallest eye apart; (2) twice their diameter or further apart	
11. Distance between PLE and AME	(0) Two × the diameter of the smallest eye or further apart; (1) between 1 and 2 × the diameter of the smallest eye apart; (2) less than the diameter of the smallest eye apart	
12. PME shape	(0) PME rounded; (1) PME oval (Jocqué and Henrard 2015*a*, fig. 4F)	
13. AME size	(0) Sub-equal or slightly larger, less than twice the diameter of the PME (Henrard and Jocqué 2015*a*, fig. 74); (1) the largest, up to 2 × the diameter of the PME (Fig. 15*C*, *D*, *F*; Jocqué and Henrard 2015*a*, fig. 4F)	
14. Clypeus height	(0) High: more than two × diameter of AME; (1) low: less than two × the diameter of AME	
15. Sternum length	(0) Longer than wide; (1) as wide as long or wider than long	
16. Sternum margins	(0) Flat; (1) rebordered (Jocqué 1987, fig. 16)	
17. Intercoxal triangular extensions	(0) Absent; (1) present (Figs 12*E*, 34*B*)	
18. Endites with meso apical modified setae	(0) Absent; (1) present (Figs 5*F*, *G*, 3*C*, *D*)	
19. Meso apical modified setae of endites	(0) Uniseriate (Figs 5*F*, *G*, 3*E*, *F*); (1) biseriate with ventral tooth (Fig. 3*C*, *D*; Henrard and Jocqué 2015, fig. 40); (2) biseriate with dorsal tooth (Fig. 3*A*, *B*)	
20. Chilum	(0) Single (Figs 27*E*, *H*, 34*B*); (1) absent or poorly developed	
21. Chilum, central projection	(0) Present (Henrard and Jocqué 2015, fig. 3); (1) absent	
22. Chilum, inferior margin	(0) Straight or concave; (1) convex	

(*continued next page*)

Table 2. (*continued*)

Character	States	Notes
23. Chelicerae, dorsal side of paturon	(0) With anteromesal group of hairs, rare elsewhere (Fig. 15*C*); (1) with scattered hairs or mediodorsal group of hairs (Jocqué and Henrard 2015, fig. 4C)	
24. Chelicerae, anteromesal cusp	(0) Absent; (1) present, with one small tooth (Jocqué 1991, fig. 2; Szüts and Jocqué 2001, fig. 4)	
25. Teeth on retromargin (posterior margin) of chelicerae	(0) Without teeth; (1) with 1 tooth only (Fig. 4*A*, *B*; Henrard and Jocqué 2015, fig. 41)	
26. Teeth on promargin (anterior margin) of chelicerae	(0) With 2 teeth (Fig. 4*A*, *B*; Henrard and Jocqué 2015, fig. 41); (1) without teeth	
27. Bugle on fang furrow	(0) Absent; (1) present at base of fang (Figs 5*H*, *I*, 12*H*)	
28. Intercheliceral triangle	(0) Absent; (1) present (Jocqué 1991, figs 345, 366, 397)	In a few taxa, the chelicerae are widely separated at the base thus forming a triangular space as seen from the front.
29. Chelicerae mobility	(0) Chelicerae free; (1) chelicerae fused basally; (2) chelicerae fused near the middle or in the distal half	Chelicerae are most often independent but may be fused. This is clearly seen from the ventral side and is indicated by a rectangular sclerotisation.
30. Cheliceral condyle	(0) Present; (1) absent	
31. Inner face of chelicerae	(0) Rounded; (1) flat	The transect of a paturon is oval in most spiders. This is also the case in most zodariids. In a few taxa it is roughly triangular because the inside is flat.
32. Preening brush with chisel-shaped setae on metatarsi II or III	(0) Present (Fig. 7*A*, *B*; Jocqué 1991, figs 6, 7; Henrard and Jocqué 2015, figs 82); (1) absent	The shape of the preening brush setae, if present, are very particular in several genera and characterised by a chisel shape in the sense that they are cylindrical at the base and flat in the distal part. Cylindrical setae are usually provided with short barbs.
33. Femoral organ on leg I	(0) Absent; (1) one; (2) two (Figs 8*B*, *C*, 4*C–F*; Henrard and Jocqué 2015, fig. 18)	
34. Femoral organ on leg II	(0) Absent; (1) one; (2) two (Figs 8*B*, *C*, 4*C–F*; Henrard and Jocqué 2015, fig. 18)	
35. Femoral organ on leg III	(0) Absent; (1) one; (2) two (Figs 8*B*, *C*, 4*C–F*; Henrard and Jocqué 2015, fig. 18)	
36. Femoral organ on leg IV	(0) Absent; (1) one; (2) two (Figs 8*B*, *C*, 4*C–F*; Henrard and Jocqué 2015, fig. 18)	
37. Femoral organ, shape of setae	(0) Conical, simple or slightly incised (Figs 8*D–I*, 4*D*, *G*; Henrard and Jocqué 2015, figs 19, 20); (1) barbed (Jocqué and Henrard 2015*a*, figs 13E, 16G)	
38. Tibia, apical prolateral process	(0) Present, well visible (Fig. 7*H*; Jocqué and Henrard 2015*b*, figs 17A-E); (1) inconspicuous, hidden under the T-Mt joint (Jocqué and Henrard 2015*b*, figs 19E, F, 20A, B)	The tibial process (Jocqué and Henrard 2015*b*) is a remarkable character that appears to be synapomorphic for the zodariid family. In some 'derived' taxa the tibial process is less prominent and may be hidden under the T-Mt joint.
39. Hinged hairs	(0) Present (Jocqué 1991, fig. 13); (1) absent	Hinged hairs are large dark setae with a particular hinge socket that allows a large array of positions. More than one hinged hair per leg is considered numerous.
40. Flattened incised hairs on legs	(0) Absent; (1) present (Fig. 4*F*)	A type of hairs that is common in derived zodariids.
41. Spination on legs III and IV	(0) Completely developed; (1) reduced in numbers; (2) absent	The fully developed spination on the hind legs consists of two or three dorsal spines on the femora, one or a few spines on the patellae, two or three dorsal, pro- and retrolateral and five or more ventral spines on the tibiae, six or more dispersed spines and a distal whorl on the metatarsi. In several taxa the number is reduced, often to a few dorsal femoral spines, and in some taxa there are no spines at all.
42. Spination and hair cover on anterior leg pairs	(0) Much weaker and less dense than on legs III and IV; (1) spination similar to that on legs III and IV	

(*continued next page*)

Table 2. (*continued*)

Character	States	Notes
43. Tibia and/or metatarsus of anterior leg pair of male	(0) With ventral rows of long spines; (1) without ventral spine rows	
44. Tarsus, spiniform ventral cover	(0) Present (Jocqué 1991, figs 4, 5); (1) absent	Scopulae are often absent but sometimes the ventral side of the tarsus may be provided with rows of thin spines and/or spiniform setae, a cover called here 'spiniform', often more pronounced on tarsus III and IV.
45. Patellar crack	(0) Absent; (1) present (Jocqué and Dippenaar-Schoeman 1992, fig. 5)	Several genera have a ring-shaped area in the patella that allows autotomy. Most specimens in collections therefore lack several legs from the base of the patella onwards.
46. Shape of anterior tarsi	(0) Cylindriform; (1) fusiform or slightly widened towards tip	The anterior tarsi may be either cylindriform and as wide at the base as at the tip or fusiform. In that case, they are widest in the middle but in some cases the tarsi are wider at the tip than at the base.
47. Tarsi, distally with subdistal suture	(0) Absent; (1) present	In some Zodariinae, the tarsi have a subdistal suture that is visible as a faint lighter ring, especially in ventral and lateral stereomicroscope views. The feature is also present in several other families (Ramírez 2014, figs 59E, F, 60F, G).
48. Tarsi, row of trichobothria increasing in length towards tip	(0) Present (Dippenaar-Schoeman and Jocqué 1997, fig. 35e); (1) absent	The presence of a row of trichobothria is a well known character in the Agelenidae. In Zodariidae, there is apparently a tendency towards the loss of the character with a stage where only two trichobothria are left, which is still scored as 'present'.
49. Femora, dorsal swelling at basal spine	(0) Absent; (1) present (Dankittipakul and Jocqué 2004, fig. 43)	In some taxa, the base of the femora is raised at the insertion of the basal spine. The swelling may correspond with a file of a stridulating organ in some species (Jocqué 2005, figs 15–16).
50. Female palpal tarsus, shape	(0) Conical; (1) cylindrical (Jocqué and Henrard 2015*a*, figs 5D, E)	
51. Female, palpal claw, orientation	(0) Turned inward over less than 45° (Jocqué and Henrard 2015*a*, fig. 5E); (1) turned inward over more than 45°	The position of the female palpal claw is turned inward in many zodariids. This character is exceptional in spiders.
52. Female, prolateral spination of palpal tarsus	(0) With numerous spines; (1) without or very few spines	Prolateral palpal spination is variable. It is considered as numerous when more than two spines are present.
53. Female, ventro-retrolateral spination of palpal tarsus	(0) With numerous spines; (1) absent or very few (one at the most)	When the spines are present, they are usually located mainly on the ventro-prolateral side of the tarsus.
54. Female palp with patch of chemosensitive hairs	(0) Absent; (1) present (Jocqué and Henrard 2015*a*, fig. 5E)	
55. Female, palpal tarsus, dorsal trichobothrium	(0) Absent; (1) present dorsally	
56. Female, palpal tarsus, retrolateral trichobothrium	(0) Present; (1) absent	
57. Abdomen, shape in lateral view	(0) Oval (Fig. 12*G*); (1) posteriorly widened (Jocqué 1991, figs 334, 354)	The shape of the abdomen is most often oval and longer than high but in some taxa it may be widened posteriorly or higher than long.
58. Male ventral abdominal scutum	(0) Absent; (1) present (Jocqué 2011, figs 5, 7)	
59. Female sub-epigastric scutum	(0) Absent; (1) present (Jocqué 1991, fig. 325)	
60. Modified hairs in front of tracheal spiracle	(0) Absent; (1) rows or field of strong spiniform hairs (Dankittipakul *et al.* 2012, figs 122–125; Dankittipakul and Jocqué 2004, figs 2, 3); (2) row of setiform or flattened hairs (Jocqué and Henrard 2015*a*, fig. 5F)	
61. Dorsum of abdomen with deep groove in male	(0) Absent; (1) present (Henrard and Jocqué 2015, figs 26, 65)	Species of the genus *Suffrica* have a modified abdomen that is provided with a deep longitudinal groove in the male.

(*continued next page*)

Table 2. (*continued*)

Character	States	Notes
62. Abdomen with frontal lateral apodemes	(0) Present (Jocqué 1999, figs 32, 33); (1) absent	Near the frontal curve on either side of the abdomen, there is a lateral apodeme in most zodariids.
63. Ventral side of the abdomen	(0) With hinged hairs; (1) without hinged hairs	In some taxa, the ventral side of the abdomen is provided with long dark hairs of the same type as described in character 39.
64. Epiandrum	(0) Present (Jocqué 2009, fig. 16); (1) absent	The male genital area is covered with a sclerotised plate in many zodariids.
65. Posterior lateral spinnerets (PLS) in males	(0) Short; (1) absent (Fig. 6*C*)	The males' PLS vary a lot: in the plesiomorphic state they are well developed whereas they become stunted or even absent in more derived taxa.
66. Posterior median spinnerets (PMS) in males	(0) Short; (1) absent (Jocqué and Baert 2005, fig. 5)	Similar to the PLS, the males' PMS vary a lot: in the plesiomorph state they are well developed whereas they become stunted or even absent in more derived taxa.
67. PMS in females	(0) Normal, similar to PLS; (1) short	The females' PMS go through a similar evolutionary sequence as in the males but they are never absent.
68. PLS and PMS of female, large cylindrical gland spigots	(0) Present (Ramírez *et al.* 2014, figs 6E, F); (1) absent	
69. Male palp, tibial apophyses	(0) RTA only; (1) both RTA and DTA (Henrard and Jocqué 2015, figs 5, 16, 29, 33)	
70. Male palp, embolus, shape	(0) Long and rigid or whip like (Figs 9*A*, *B*, 16*B*); (1) short and rigid (Fig. 13*B*; Jocqué and Henrard 2015*a*, fig. 10E)	The length of the embolus is a very flexible character as has been shown many times (Jäger 2006; see Jocqué *et al.* 2013 for an overview). The polarity of this character will greatly depend on the choice of the outgroup.
71. Origin of the embolus	(0) On the posterior end of the tegulum or retrolateral (Henrard and and Jocqué 2015, figs 32, 70); (1) on the prolateral side or in the centre of the tegulum (Figs 9*A*, *B*, 13*B*, 6*B*; Jocqué and Henrard 2015*a*, fig. 10E)	The origin of the embolus may seem difficult to determine but in general it is clear cut. In rare cases it originates in the centre of the tegulum (e.g. *Amphiledorus*).
72. Cymbium, deep lateral fold	(0) Absent; (1) present (Dankittipakul and Jocqué 2004, fig. 53; Dankittipakul *et al.* 2012, fig. 69)	The cymbial fold appears to be one of the solutions to support a long embolus.
73. Cymbium, basolateral flange or process	(0) Absent; (1) present (Figs 9*C*, 13*C*, 16*C*)	The basolateral margin of the cymbium may be thickened and slightly protruding ventrally, forming a flange. In some cases the basolateral flange may be extended backwards and forms a spoon-shaped extension.
74. Axis of cymbium (in lateral view)	(0) straight or slightly curved; (1) strongly curved	Both margins of the cymbium have to be curved. It doesn't count if only one margin of the cymbium is curved.
75. Male cymbium with prolateral spines	(0) With dispersed spines; (1) absent or very few	
76. Palpal terminal spine	(0) Present;(1) absent	
77. Male, palpal tarsus with modified prolateral setae	(0) Absent; (1) present, conspicuous and pectinate (Russell-Smith and Jocqué 2015, fig. 15; Jocqué and van Harten 2015, fig. 34)	As the character is present and equal in both sexes, it is mentioned only under Male palp to avoid redundancy.
78. Cymbium, distal part (when viewed ventrally or dorsally)	(0) Tapered apically (Jocqué and Henrard 2015*a*, fig. 10*E*); (1) rounded apically (Figs 13*B*, 16*B*; Henrard and Jocqué 2015, figs 28, 70)	

is variable within the SF clade. The ambiguity problem can be resolved by choosing either fast or slow optimisation (Fig. 2*A*, *B* respectively). Given that the number of derived characters defining the DF clade rises from 4 to 6 (slow optimisation) or 7 (fast optimisation), the low support value (51/1) is surprising although this group has numerous homoplasies (Figs 1, 2*A*, *B*).

Members of the DF clade are also characterised by some modified setae on the mesoapical part of the endites (18–1), which can be either claw-shaped such as in the new genus *Suffascar* (Figs 3*E*, *F*, 5*F*, *G*) or biseriate with a tooth that can be either dorsal as in *Suffasia* and *Asceua* (Fig. 3*A*, *B* respectively) or ventral as found in *Suffrica* (Fig. 3*C*, *D*; Henrard and Jocqué 2015, fig. 40). Such modified setae on the endites were not observed (including by SEM) in taxa of the SF clade, nor in the other 'outgroups' of the analyses. However, the range of setae on the endites (including the modified setae) in other taxa may provide useful phylogenetic information and workers should continue to record these in descriptions.

Taxa of the DF clade also share some plesiomophic characters, such as the presence of two cheliceral teeth on the promargin (26–0; Figs 4*A*, *B*, 5*I*; Henrard and Jocqué 2015, fig. 41). Although 'derived' in the present analysis, the sole tooth on the retromargin (25–1) as found in *Suffasia* (Fig. 4*A*), *Asceua* (Fig. 4*B*) and *Suffrica* (Henrard and Jocqué 2015, fig. 41) seems to have been replaced by a ridged bugle in *Suffascar* (27–1) (Figs 5*H*, *I*, 12*H*).

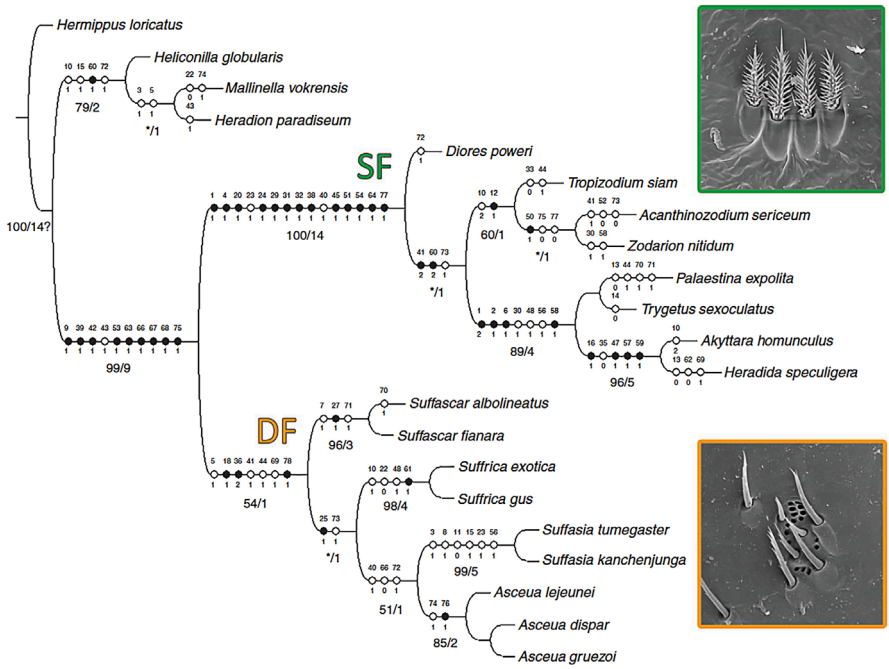

Fig. 1. Unique most parsimonious tree obtained from the 'ratchet' search in Winclada with tree lenth = 150, consistency index = 59 and retention index = 85. Black circles indicate non-homoplasious, white circles homoplasious changes (unambiguous changes only). Character numbers are placed above the circles and the states are shown under the circles. The numbers below the branches indicate the Bootstrap value / Bremer support (Bp/Br). Branches with no support (Bp <50; Br <1) are indicated by an asterisk or not shown if both are below mentioned values. DF: dual femoral organ clade; SF: single femoral organ clade. The image on top shows the single prolateral femoral organ II of *Zodarion nitidum* (Audouin, 1826) belonging to the SF clade (in green); the image below shows the prolateral femoral organ II of *Suffascar fianara*, gen. et sp. nov. from the DF clade (in orange).

These preliminary insights into the importance of the femoral organ in the phylogeny of these groups need to be tested in a broader context, for example by sampling taxa from other genera and outgroups. With further investigation, there might be enough evidence to re-establish the subfamily 'Storeninae', which could be diagnosed by the presence of chisel-shaped setae in the preening brushes in combination with the absence of femoral organs.

Taxonomy

Suffascar, gen. nov.

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Type species: *Suffascar fianara*, sp. nov.

Diagnosis

Suffascar, gen. nov. is part of the dual femoral organ clade (DF) together with *Asceua*, *Suffasia* and *Suffrica* (Figs 1, 2*A*, *B*; see also Henrard and Jocqué 2015). It can be distinguished by the ridged bulge on the dental groove of the plastron at the base of the fang (Figs 5*H*, *I*, 12*H*), the clawed medial setae on the endites (Fig. 5*F*, *G*) and by the tiny PME along with the large AME, especially pronounced in males (Figs 5*C*, 15*C*, *D*, 27*D*, *F*). Males are further characterised by the cymbium with pro- and retrolateral basal processes (prolateral cymbial process and retrolateral cymbial process; Figs 9*C*, *D*, 13*A*–*C*, 14*A*, *B*) and a row of modified ventral setae just in front of the bulbus (Figs 13*B*, 14*A*). Females are characterised by the presence of a pair of membranous bladders in the vulva (Figs 10*B*, *C*, 16*D*, *E*).

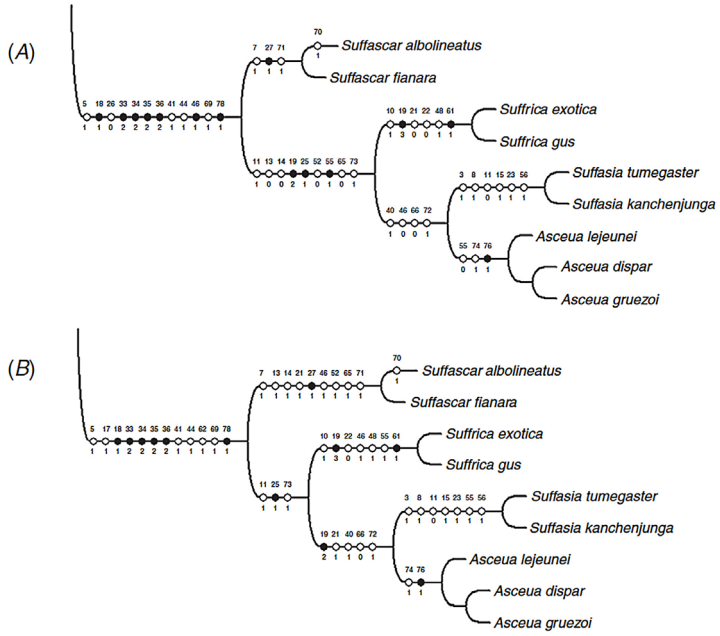

Fig. 2. Detail of the dual femoral gland clade (DF) using either (*A*) fast optimisation or (*B*) slow optimisation. Black circles indicate non-homoplasious changes, white circles homoplasious changes. Character numbers are placed above the circles; states are shown under the circles.

Description

Small spiders (1.5–2.6, one species 4.7) with smooth to slightly reticulated teguments (Figs 5*A*, *C*, *D*, 15*B*, *G*).

Colour (Figs 12, 15, 21, 24, 27, 30–32, 34, 37). Carapace, mouthparts and sternum shades of orange to brick-red; legs shades of yellow to white; abdomen dorsum shades of sepia often with median paler stripe, sides and venter cream.

Carapace (Figs 5*A*, 14*A–C*, *F*, 12*A*, *C*, *D*, 32*A*, *B*, *C*, 37*A*, *C*, *D*) pear-shaped to ovoid or quadrangular, longer than wide (L/W <1.4–1.6), devoid of setae, widest at level of coxae 2–3, narrowed to ~0.64–0.72× maximum width in eye region (cephalic width measured on posterior tangent of PME). Cervical grooves poorly indicated in some species. Profile: high, strongly domed, height ~3/4 of width, culminating at level of coxae 1–2. Fovea short, in shallow depression.

Eyes (Figs 5*A*, *C*, *D*, 12*B*, 24*D*, *H*, *I*, 32*C*) in two procurved rows. AME dark, the largest; PME the smallest; ALE and PLE subequal; AME larger in male than in female.

Clypeus convex, slightly retreating, height 1.5 to 2.5× diameter of AME. Chilum (Figs 27*E*, *H*, 34*B*) triangular, not divided, not projecting in centre and devoid of setae, sometimes faint or poorly delimited (Figs 15*E*, 30*B*).

Chelicerae conical, with few dispersed setae; intercheliceral triangle absent; dental groove with two tiny teeth on promargin and with ridged bulge at base of fangs (Figs 5*H*, *I*, 12*H*); fangs about as long as wide at base. Labium (Figs 5*E*, 22*B*, 27*I*) triangular, longer than wide, with narrowed base. Endites elongate, roughly triangular, converging, anteriorly provided with peculiar mesal, uniseriate setae (Figs 5*F*, *G*).

Sternum (Figs 5*B*, 15*E*, 34*B*) smooth to granulate, shield-shaped, slightly longer than wide, with small triangular coxal and intercoxal extensions; anterior margin straight or slightly curved in middle to accommodate base of labium; posterior extremity rounded or slightly indented.

Legs slender. Formula 4123. Three-clawed: paired claws with numerous teeth, unpaired claw toothless (Fig. 7*F*, *G*). Spination reduced to one dorsal spine on culminating, sub-basal point of all femur; two to four ventral biseriate spines on distal margin of metatarsus II–IV (Figs 7*A*, 18*A*, 34*A*). Preening brushes with chisel-shaped setae on metatarsus II and III (Figs 7*A*, *B*). No hinged hairs. No flattened, incised

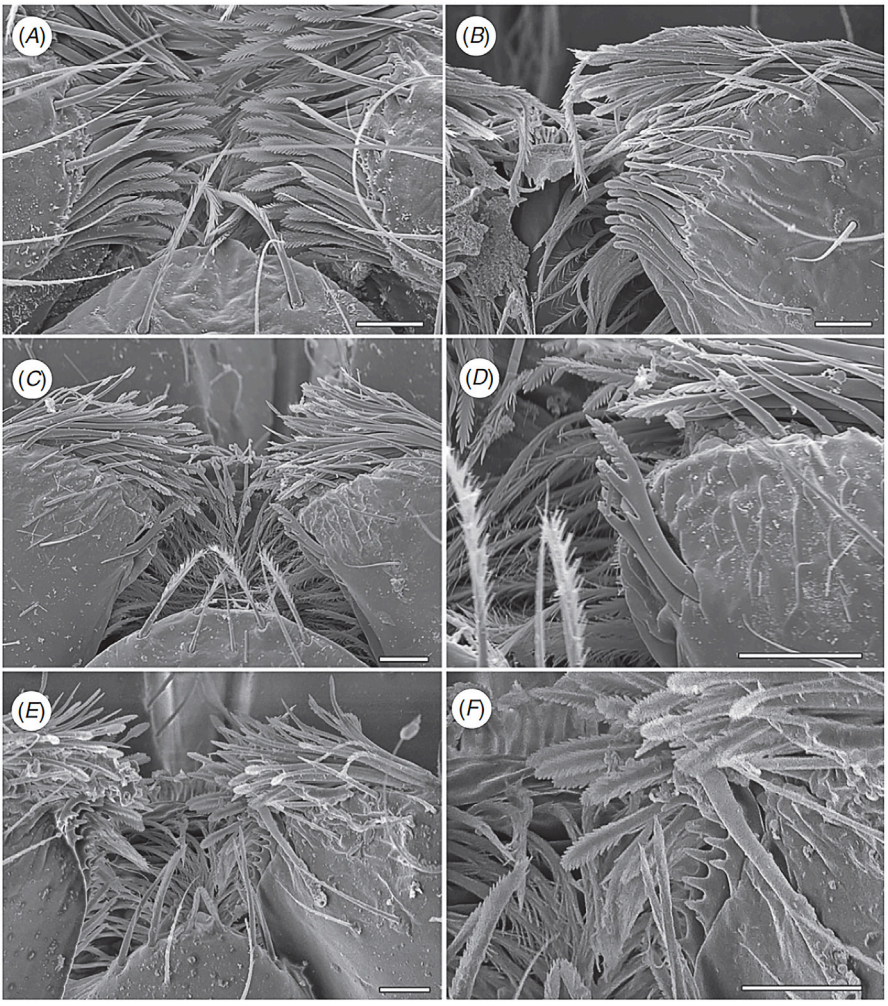

Fig. 3. Scanning electron micrographs showing modified setae on the meso-apical part of the endites, ventral view. (*A*) *Suffasia kanchenjunga* Ono, 2006, female. (*B*) *Asceua lejeunei* Jocqué, 1991, subadult female. (*C*) *Suffrica exotica* Henrard & Jocqué, 2015, female. (*D*) As previous, detail. (*E*) *Suffascar albolineatus*, gen. et sp. nov., juvenile (MRAC 245344, DNA Z100). (*F*) As previous, detail. Scale bars = 20 µm.

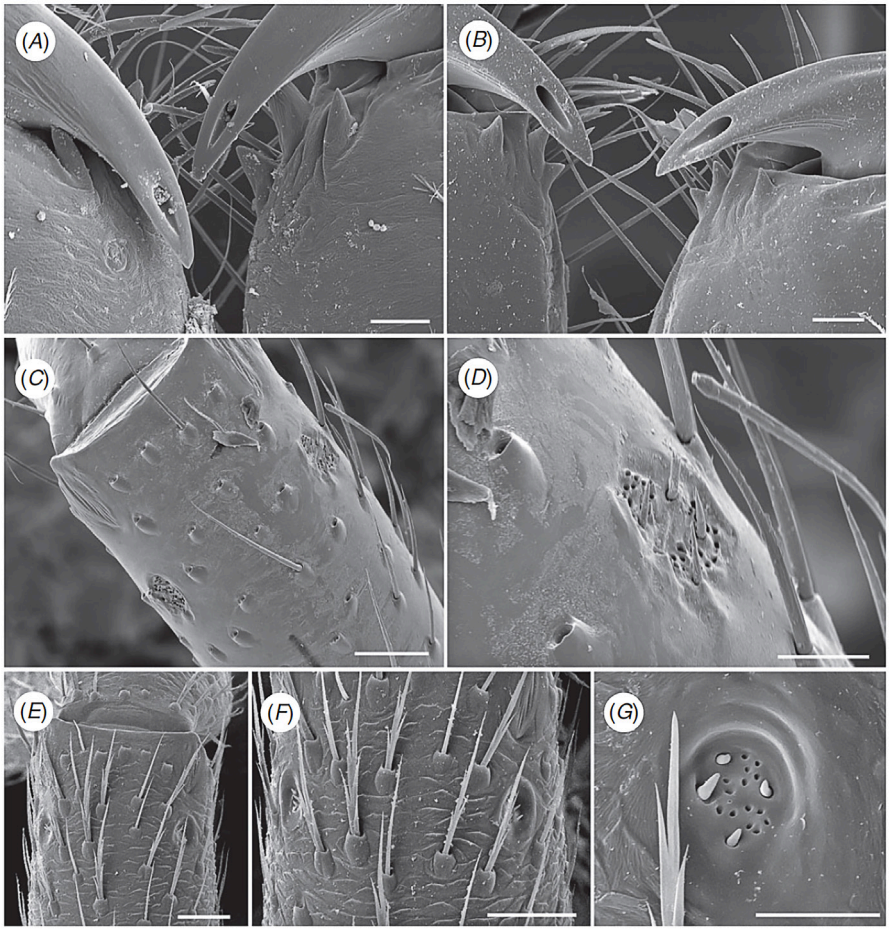

Fig. 4. Scanning electron micrographs of chelicerae and femoral organs. (*A*) *Suffasia kanchenjunga* Ono, 2006, male, detail of cheliceral teeth, ventral view. (*B*) As previous, *Asceua lejeunei* Jocqué, 1991, subadult female. (*C*) *Suffasia kanchenjunga*, male, apical part of femur I, dorsal view. (*D*) As previous, detail of the femoral organ outlet. (*E*) *Asceua* cf. *dispar* (Kulczynski, 1911), male, apical part of femur III, dorsal view. (*F*) As previous, detail. (*G*) As previous, detail of femoral organ outlet. Scale bars: A, B, D, G = 20 µm; C, E, F = 50 µm.

hairs. Trichobothria: few on tibia and metatarsus; bothria transversely ridged (Fig. 7*D*). All femur subapically with two lateral (pro- and retrolateral) femoral glands provided with conical, slightly barbed hairs and small pores in slight depression (Figs 8*A–I*, 31*E*). Tarsal organ capsulate (Fig. 7*C*). Tibial process (Jocqué and Henrard 2015*b*) present, conspicuous (Fig. 7*H*).

Female palp with conical tarsus (Figs 7*E*, 12*F*, 34*F*); with few pro-apical, barbed spines; palpal claw with ~15 teeth inserted medially (Figs 7*E*, 34*F*); turned inward over 45° (Fig. 18*G*); without distal patch of chemosensitive setae (Figs 7*E*, 34*F*).

Male palp: tibia with ventral anterior concavity (Fig. 9*D*); retrolateral tibial apophysis (RTA) small, broadly triangular to

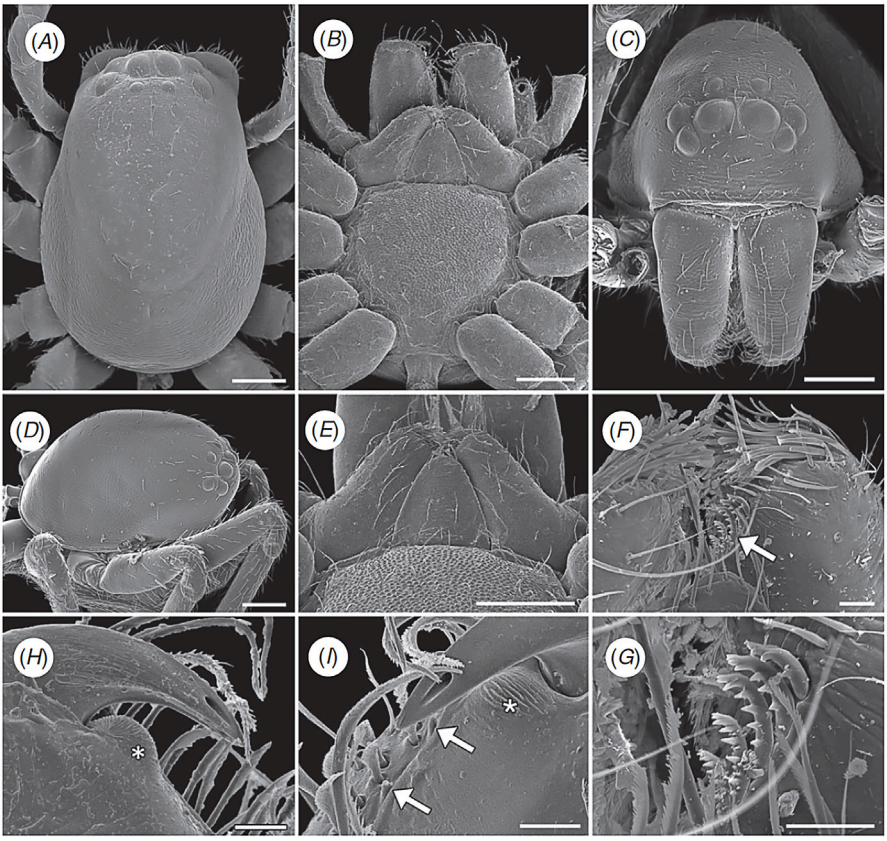

Fig. 5. Scanning electron micrographs of body parts. (*A*) *Suffascar fianara*, gen. et sp. nov., female paratype (MRAC 245353, DNA Z304), carapace, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, frontal view. (*D*) *Suffascar macromma* sp. nov., female paratype (MRAC 177964), carapace, lateral view. (*E*) *Suffascar fianara*, female paratype (MRAC 245353, DNA Z304), endites and labium, ventral view. (*F*) As previous, apical part of endites, ventral, slightly oblique view. The arrow points to the modified claw-like setae. (*G*) As previous, detail. (*H*) Same female, detail of the apical part of a chelicera, ventral view. (*I*) As previous, slightly anterior view. The arrows point to the small promarginal teeth. The stars indicate the ridged bugle at the base of the fang. Scale bars: A–E = 0.2 mm; F–G = 20 µm.

narrow, hook-shaped (Figs 13*C*, 16*C*, 19*C*); ventral tibial apophysis small, thumb like (Figs 9*C*, *D*, 13*A*–*C*, 14*A*, *B*). Cymbium with well developed basal retrolateral scoop (retrolateral cymbial process) and prolateral rounded process (prolateral cymbial process; Figs 9*C*, *D*, 13*A*–*C*, 14*A*, *B*); row of slightly modified setae on rim delimiting bulbal concavity anteriorly (Figs 13*B*, 14*A*). Embolus long and slender to fairly short, broad at base (Figs 9*A*, *B*, 13*B*, 14*A*, 25*B*, 26*A*). Median apophysis medium-sized, variable: thin, sickle or S-shaped to broad, roughly T-shaped (Figs 13*B*, 16*B*, 25*B*). Conductor (Figs 9*A*, *B*, 13*A*, *B*, 14*A*, *B*) with sclerotised ventral part and membranous dorsal part forming concavity.

Abdomen oval, without frontal or lateral apodemes. Tracheal spiracle very small. Female with six spinnerets (Fig. 6*A*, *B*);

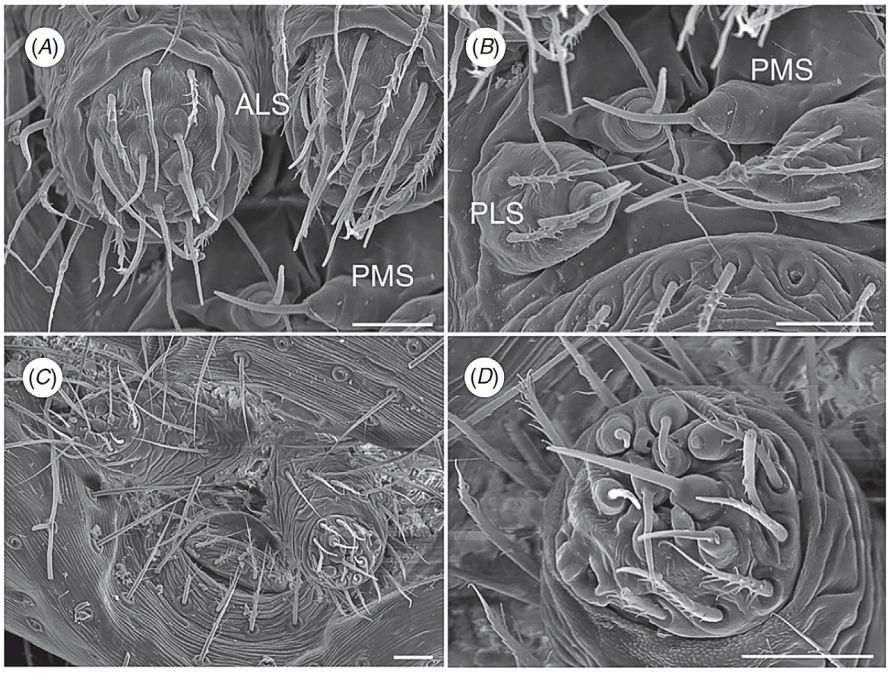

Fig. 6. Scanning electron micrographs of the spinnerets. (*A*) *Suffascar macromma*, gen. et sp. nov., female paratype (MRAC 177964), ALS, ventral view. (*B*) As previous, PMS and PLS. (*C*) *Suffascar fianara*, sp. nov., male paratype (MRAC 245343), ALS, ventral view. (*D*) As previous, detail. Scale bars = 20 µm.

males with two (Fig. 6*C–D*). ALS large, conical, biarticulate; with central major ampullate gland spigot and marginal piriform gland spigots. PLS and PMS, in female only, with cylindrical gland spigots. Colulus represented by few setae.

Epigyne (Figs 10*A–L*, 11*A–I*, 19*D–H*) fairly simple with small widely separated spermathecae and short copulatory ducts; provided with pair of membranous bladders (Fig. 10*B*, *C*), these may be translucent or dark brown and possibly plugged. Spermathecae riddled with tiny pores and with one or more large pores (Fig. 11*A*, *G*, *H*), dorsally with small rounded to scale like outgrowth (Fig. 11*C*, *F*, *I*).

Distribution

Suffascar is apparently endemic to Madagascar (Figs 38*A–D*).

Etymology

The genus name is a combination of the prefix 'Suff-' as in *Suffrica* and *Suffasia*, and the last part of Madagascar. The gender is masculine.

Key to the species of *Suffascar* – Males

1. Embolus long and slender, parallel sided, its base as wide as subapical part (Figs 16*B*, 17*A*) 2
   Embolus shorter, tapered, with base much wider than subapical part (Figs 13*B*, 14*A*, 19*B*, 20*A*, 25*B*, 26*A*) 3
2. Abdominal scutum well developed, sclerotised (Fig. 32*A*); retrolateral tibial apophysis massive, as wide as long (Figs 32*F*, 33*B*); prolateral cymbial process slender, tapered apically (Fig. 32*D*) ..... *Suffascar scutatus*
   Scutum inconspicuous; retrolateral tibial apophysis smaller, longer than wide (Figs 16*C*, 17*B*); prolateral cymbial process broader at base, apically blunt (Fig. 16*A*) ..... *Suffascar fianara*
3. Embolus roughly triangular or blade-shaped (Figs 19*B*, 20*A*, 25*B*, 26*A*) 4
   Embolus abruptly tapered in proximal half, distal half straight and thin (Figs 13B, 14A) ..... *Suffascar albolineatus*
4. Embolus triangular or fin-shaped, longitudinal fold faint (Figs 25*B*, 26*A*, 35*B*, 36*A*); median apophysis slender, sickle- or S-shaped, projecting at base (Figs 25*A*, *C*, 26*B*, 35*A*, *C*, 36*B*) 5
   Embolus blade-shaped with deep longitudinal fold (Figs 19*B*, 20*A*); median apophysis broad, roughly T-shaped (Figs 19*B*, 20*A*), not projecting at base (Figs 19*A*, *C*, 20*B*) ..... *Suffascar fisheri*

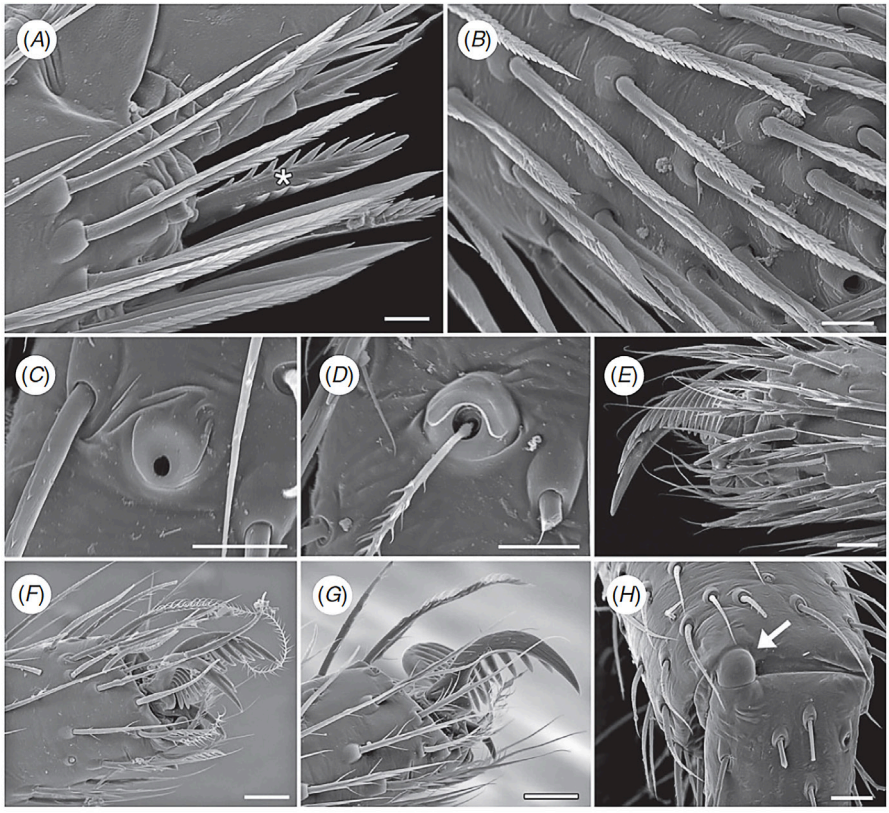

Fig. 7. Scanning electron micrographsof leg parts. (*A*) *Suffascar macromma*, gen. et sp. nov., female paratype (MRAC 177964), chisel-shaped setae and serrated terminal spines (star) of metatarsus III, retrolateral view. (*B*) *Suffascar fianara*, sp. nov., male paratype (CASENT 9003473), chisel-shaped setae of metatarsus III, ventro-lateral view. (*C*) Same male, tarsal organ of leg IV, dorsal view. (*D*) Same male, metatarsal trichobothrium of leg IV. (*E*) *Suffascar fianara*, female paratype (MRAC 245353, DNA Z304), palpal claw, prolateral view. (*F*) *Suffascar macromma*, female paratype (MRAC 177964), tarsal claw of leg I, lateral view. (*G*) As previous, leg III. (*H*) Same female, tibial process (arrow), dorsal view. Scale bars: A–D= 10 µm; E–H = 20 µm.

5. Median apophysis S-shaped, both lateral margins sinuous (Figs 25*B*, 26*A*, 28*B*, 29*A*); retrolateral tibial apophysis slender, hook-shaped (Figs 25*C*, 26*B*, 28*C*, 29*B*) 6
Median apophysis sickle-shaped, retrolateral margin straight or slightly curved, prolateral margin sinuous (Figs 35*B*, 36*A*); retrolateral tibial apophysis roughly triangular, with broad base (Figs 35*C*, 36*B*) ..... *Suffascar sufficiens*

6. AME very large, more than twice diameter of ALE (Fig. 27*D*, *F*); PLE and PME touching (or almost) the AME (Fig. 27*D*, *F*) ..... *Suffascar macromma*
AME not as large, less than twice the diameter of an ALE (Fig. 24*D*, *I*); PLE and PME clearly not touching the AME (Fig. 24*D*, *I*) ..... *Suffascar griswoldi*

Key to the species of *Suffascar* – Females

1. Carapace subquadrangular or cervical groove faintly marked (Figs 22*A*, 30*A*, 37*A*); ALE not touching AME (Figs 22*D*, 30*D*, 37*D*)..... 2
Carapace pear-shaped or ovoid, cervical groove marked (Figs 18*F*, 24*F*); ALE touching AME (Figs 12F, 24*H*, 27*H*)..... 4

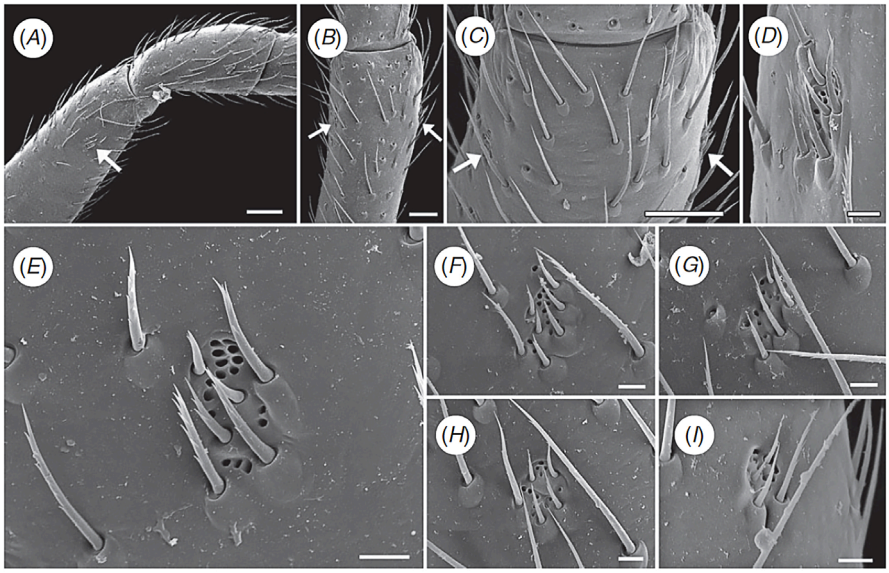

Fig. 8. *Suffascar fianara*, gen. et sp. nov., female paratype (MRAC 245353, DNA Z304), scanning electron micrographs of the dual femoral organ. (*A*) Femora and patella of leg I, prolateral view. The arrow points to the femoral gland outlet. (*B*) As previous, dorsal view. (*C*) As previous, detail, leg II. (*D*) Prolateral femoral gland outlet of leg I, lateral view. (*E*) As previous, dorsal view. (*F*) As previous, leg II, dorsal view. (*G*) As previous, leg III. (*H*) As previous, leg IV. (*I*) As previous, prolateral, lateral view. Scale bars: A = 0.1 mm; B, C = 50 µm; D–I = 10 µm.

2. PME light, strongly reduced (Figs 22*D*, 30*D*); central plate of epigyne large, strongly sclerotised and complex (Figs 23*A–C*, 30*E–H*) 3
   PME dark, not strongly reduced (Fig. 37*D*); central part of epigyne narrower, not strongly sclerotised excepted posterior rim, without any complex structures (Fig. 37*E*) ..... *Suffascar tofti*
3. Endite and labium elongate (Fig. 22*E*); spermathecae close to epigastric fold (Figs 23*A–E*) ..... *Suffascar gigas*
   Endite and labium not elongate (Fig. 30*B*); spermathecae at a distance from epigastric fold (Figs 30*E–K*) ..... *Suffascar micromma*
4. Epigyne as a sclerotised triangular plate (Figs 13*D–F*, 14*C*, 19*D–F*, 20*C*), narrower in front than near posterior rim 5
   Epigyne not or faintly sclerotised, roughly oval or quadrangular wider in front than behind 6
5. Epigyne wider than long (Fig. 13*D–F*); spermathecae large, separated from each other by 1 to 1.5 × their diameter (Fig. 13*G–I*) ..... *Suffascar albolineatus*
   Epigyne as long as wide (Fig. 19*D–F*); spermathecae smaller, separated from each other by more than 2 × their diameter (Fig. 19*G*, *H*) ..... *Suffascar fisheri*
6. Epigyne with groove along posterior margin (Fig. 25*D–F*, 29*D–F*), the latter with heavily sclerotised transverse plate (Figs 25*G–I*, 29*G–I*) 7
   Central plate of epigyne not delimited by grooves, without or faintly sclerotised transverse plate (Figs 21*C–G*, 31*F–J*) 8
7. PME separated from AME from more than its radius (Fig. 24*H*); metatarsus III–IV with three distal ventral spines ..... *Suffascar griswoldi*
   PME separated from AME from less than its radius (Fig. 27*G*, *H*); metatarsus III with four and metatarsus IV with two distal ventral spines ..... *Suffascar macromma*
8. Abdomen with dorsal white band (Fig. 21*A*, *B*); legs pale, whitish; anterior tarsi cylindrical 9
   Abdomen uniform (Figs 31*A*, 34*E*); legs not pale, yellow; anterior tarsi fusiform (Figs 31*B*, 34*F*) 10
9. Copulatory entrances close to each other (Fig. 10*A*); epigynal bladders strongly developed, close to each other (Figs 10B, 16*D*, *E*, 31*F–J*) ..... *Suffascar fianara*
   Copulatory entrances widely separated (Figs 21C–E); epigynal bladders smaller, far apart (Fig. 21*F*, *G*) ..... *Suffascar fitzpatrickae*
10. Palpal claw not strongly developed (Fig. 31*B*); epigynal bladders strongly developed, close to each other (Fig. 31*F–J*) ..... *Suffascar nonus*
    Palpal claw strongly developed (Fig. 34*F*); epigynal bladders smaller, far apart (Figs 34*G*, 36*C*) ..... *Suffascar sufficiens*

Suffascar albolineatus, sp. nov.

(Figs 3*E*, *F*, 12*A–H*, 13*A–I*, 14*A–C*, 38*B*)

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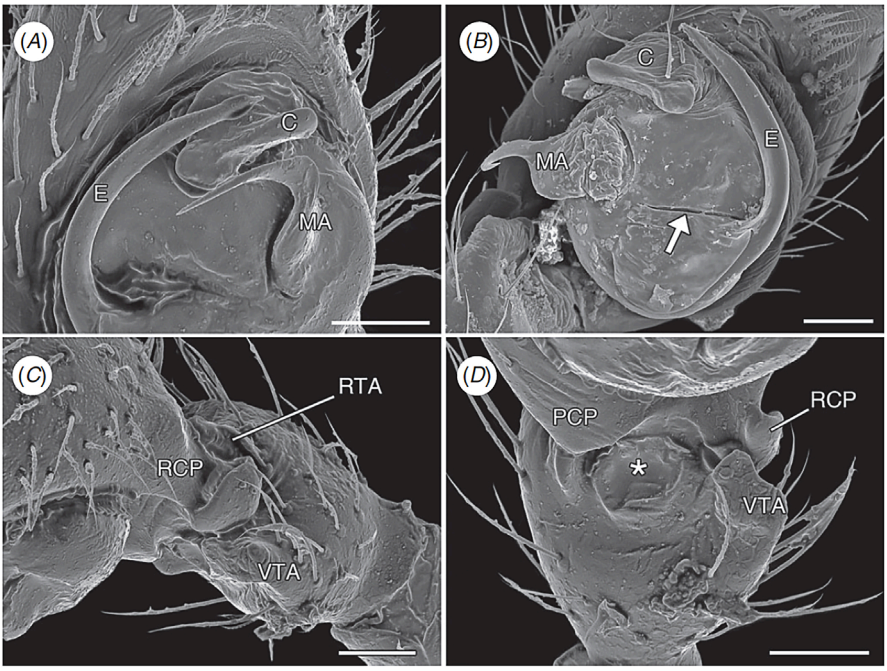

Fig. 9. *Suffascar fianara*, gen. et sp. nov., male paratype (MRAC 245352, DNA Z302), scanning electron micrograph of palp. (*A*) Bulbus of left palp, ventral view. (*B*) As previous, right palp (note the median apophysis out of its normal position). The arrow shows the groove at the base of the embolus. (*C*) Tibia and base of cymbium, retrolateral view. (*D*) As previous, ventral view. The star indicates the tibial ventral concavity. C: conductor; E: embolus; MA: median apophysis; PCP: prolateral cymbial process; RCP: retrolateral cymbial process; RTA: retrolateral tibial apophysis; VTA: ventral tibial apophysis. Scale bars = 50 µm.

Material examined

Holotype. MADAGASCAR: ♂, Fianarantsoa Province: P.N. Ranomafana, Talatakely, 1.68 km SW Ranomafana, 21.25041°S, 47.41945°W, 900 m asl, 4–16.i.2001, pitfall traps, mixed tropical forest, D.H. & K.M. Kavanaugh, R.L. Brett, E. Elsom & F. Vargas (CASENT 9003430).

Paratypes. **MADAGASCAR**: Fianarantsoa Province: 3 ♀, 1 juvenile, P.N. Ranomafana, Talatakely, 1.68 km SW Ranomafana, 21°15′50.6″S, 47°9.6′E, 970 m asl, 11–12.i.2009, Berlese extraction of leaf litter, primary montane rainforest, C. Griswold, G. Hormiga, A. Saucedo & H. Wood (CASENT 9031095) (1 ♀, 1 juvenile in MRAC 245344; juvenile DNA Z100); 1 ♂, as preceding (MRAC 245345, ex. CASENT 9003429); 1 ♀, 29 km SSW of Ambositra, Ankazomivady, 20°46.6′S, 47°09.9′E, 1700 m asl, 7.i.1998, pitfall traps, forest, B.L. Fisher (CASENT 9076860); 1 ♂, as preceding (CASENT 9076861); 2 ♀, sifted leaf litter, forest, further as preceding; 1 ♀, P.N. Ranomafana, 21°12′S, 47°27′E, iv.1992, forest, from foliage, V. & B. Roth, S. Kariko (CASENT 9076862).

Diagnosis

The male of *S. albolineatus* is recognised by the shape of the embolus, broad at base and thin in the distal half, and the median apophysis with the shape of an ice axe (Figs 13*B*, 14*A*). The female is characterised by the epigyne with transverse oval area showing dark spermathecae and pale bladders in transparency (Figs 13*D–F*, 14*C*).

Description

Male (holotype)

Total length 1.99; carapace 1.09 long, 0.60 high, 0.77 wide, narrowed to 0.51 in eye region.

Colour (Fig. 12*A*, *B*, *H*). Carapace, chelicerae and sternum uniform pale orange; dark oval area in front of AME and dark rings around all eyes except PME, which have dark triangle in

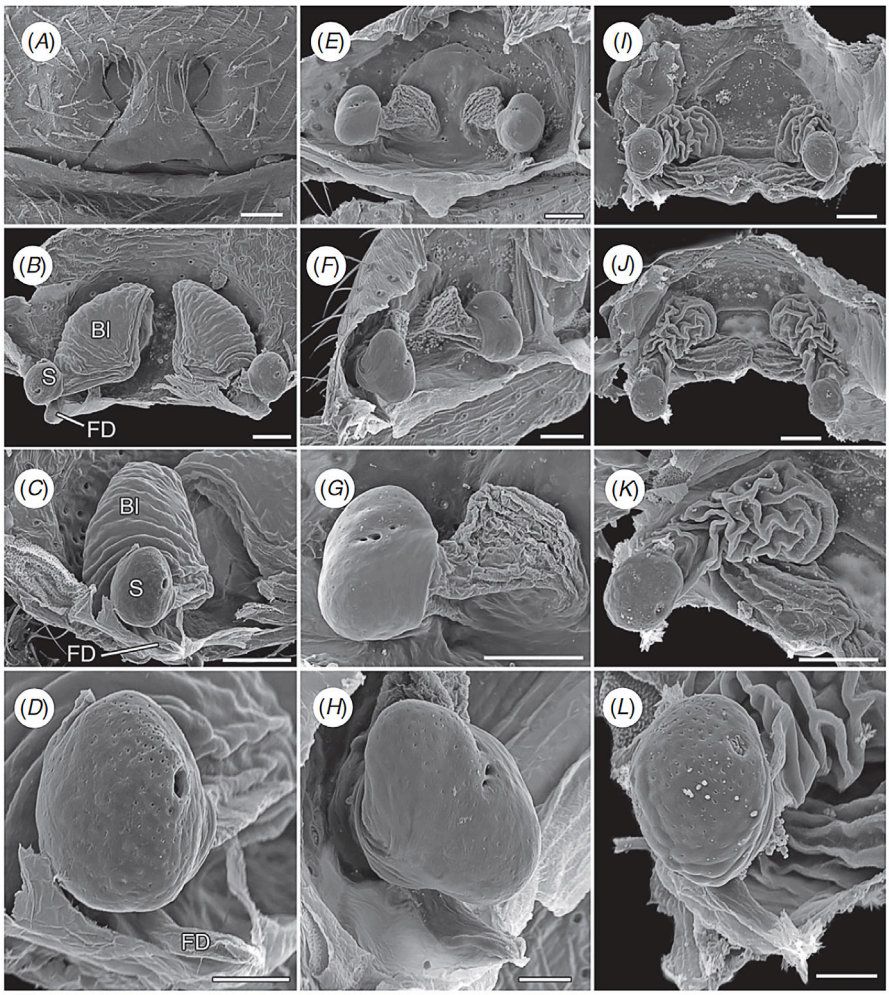

Fig. 10. Scanning electron micrograph of female genitalia. (*A*) *Suffascar fianara*, gen. et sp. nov., paratype (MRAC 245353, DNA Z304), epigyne, ventral view. (*B*) Vulva, dorsal view. (*C*) As previous, close up, latero-dorsal view. (*D*) As previous, detail of the spermatheca. (*E*) *Suffascar fisheri*, sp. nov., paratype (MRAC 245354), vulva, dorsal view. (*F*) As previous, latero-dorsal view. (*G*) As previous, close up, dorsal view. (*H*) As previous, detail of the spermatheca, latero-dorsal view. (*I*) *Suffascar macromma*, sp. nov., paratype (MRAC 177964), vulva, dorsal view. (*J*) As previous, antero-dorsal view. (*K*) As previous, close up. (*L*) As previous, detail of the spermatheca, latero-dorsal view. BI: bladder; FD: fertilisation duct; S: spermatheca. Scale bars: A–C, E–G, I–K = 50 µm; D, H, L = 20 µm.

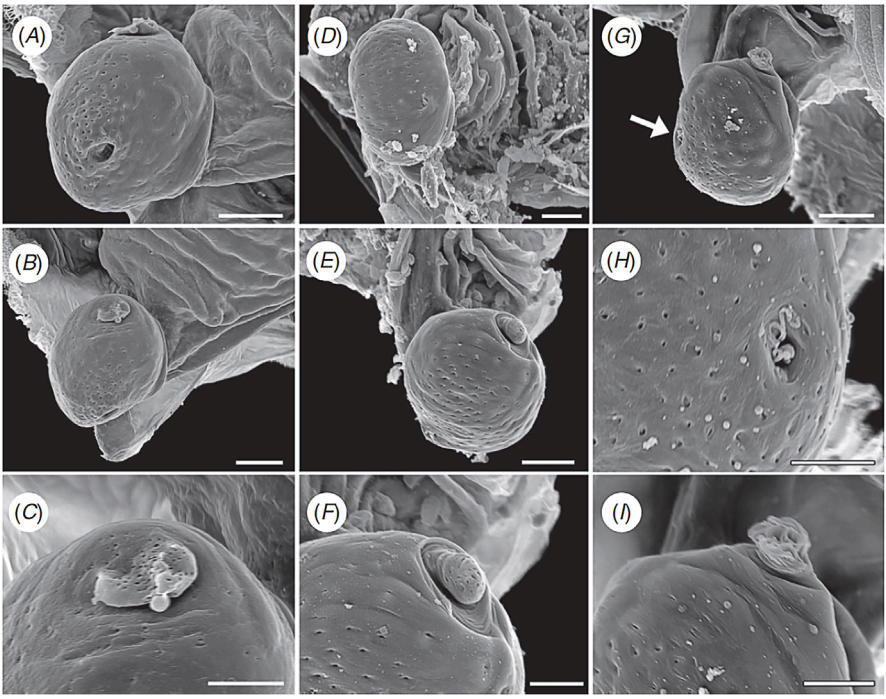

Fig. 11. Scanning electron micrograph of female genitalia. (*A*) *Suffascar fianara*, gen. et sp. nov., paratype (MRAC 245353, DNA Z304), left spermatheca, medial view. (*B*) As previous, anterior view. (*C*) As previous, detail. (*D*) *Suffascar griswoldi*, sp. nov., paratype (MRAC 245356), left spermatheca, dorsal view. (*E*) Right spermatheca, anterior view. (*F*) As previous, detail. (*G*) *Suffascar macromma*, sp. nov., paratype (MRAC 177964), right spermatheca, anterior view. The arrow points to the large medial pore. (*H*) As previous, detail, medial view. (*I*) As previous detail, anterior view. Scale bars: A, B, D, E, G = 20 µm; C, F, H, I = 10 µm.

front of them. Legs pale, almost white, tarsus pale orange. Abdomen: dorsum pale sepia with ill-defined median pale stripe; venter pale, vaguely suffused with sepia.

Carapace (Fig. 12*B*). Cephalic area smooth, thoracic area reticulate; cervical grooves slightly marked.

Eyes. AME: 0.10; ALE: 0.08; AME–AME: 0.02; AME–ALE: 0.02; PME: 0.04: PLE: 0.06; PME–PME: 0.05; PME–PLE: 0.08.

Clypeus. 0.13, 1.6 × width of ALE. Chilum a vaguely delimited triangle.

Sternum. Granulate, shield-shaped, 0.57 long, 0.51 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–IV with three distal ventral spines; metatarsus II and III with preening brush.

Leg measurements. Femur: I 0.74, II 0.66, III 0.62, IV 0.85; patella: I 0.33, II 0.31, III 0.28, IV 0.34; tibia: I 0.54, II 0.48, III 0.41, IV 0.64; metatarsus: I 0.51, II 0.49, III 0.49, IV 0.77; tarsus: I 0.49, II 0.44, III 0.33, IV 0.52; Total: I 2.61, II 2.38, III 2.13, IV 3.13.

Male palp (Figs 13*A–C*, 14*A*, *B*). Retrolateral tibial apophysis parallel-sided, pointing straight forward ending in tapered tip, curved up thence downward; cymbium basally with well developed prolateral process and large scoop-shaped retrolateral extension, distally with one small spine and ventrally row of sinuous setae near rim delimiting bulbus anteriorly; embolus with broad base and thin distal half slightly curved inward; median apophysis ice axe-shaped with blade pointing retrolaterad, hidden by conductor, which is wider than long with sclerotised tip pointing prolaterad.

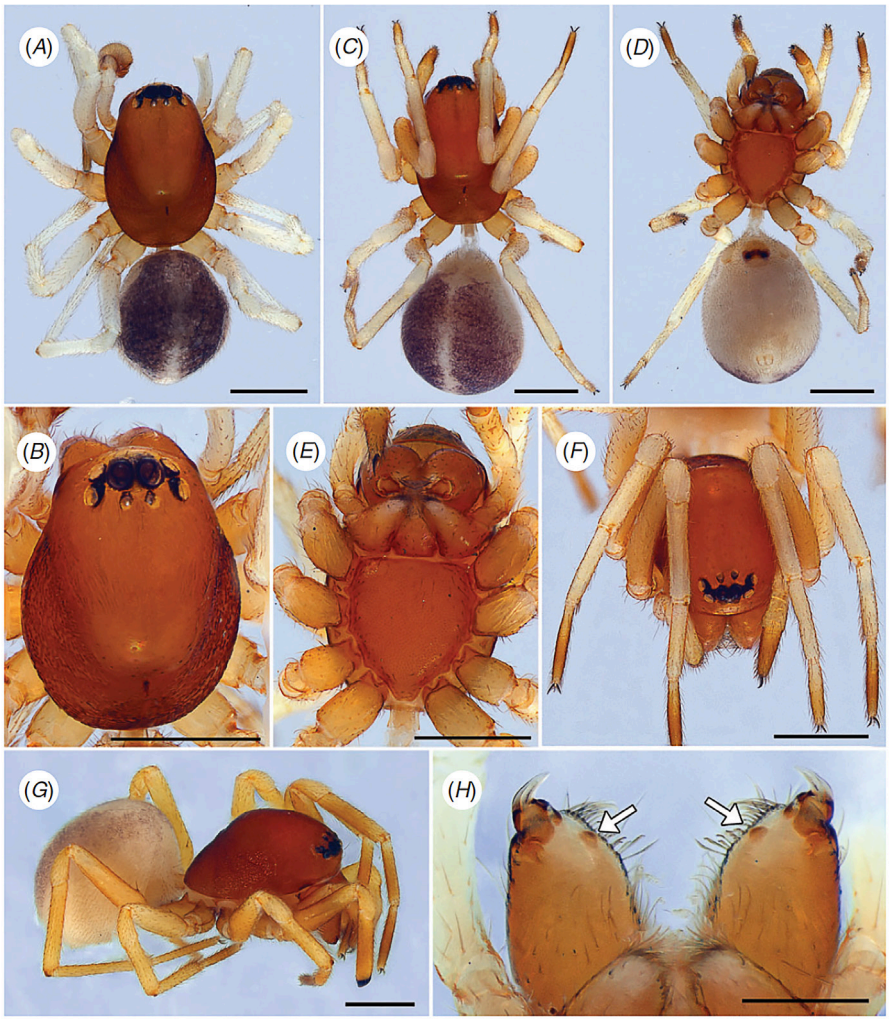

Fig. 12. *Suffascar albolineatus*, gen. et sp. nov. (*A*) Male holotype, habitus, dorsal view. (*B*) As previous, detail of carapace. (*C*) Female paratype (CASENT 9031095), habitus, dorsal view. (*D*) As previous, ventral view. (*E*) As previous, detail of prosoma. (*F*) Same female, frontal, slightly anterior view. (*G*) Other female (CASENT 9076862), lateral view. (*H*) Male holotype, chelicerae, ventral view. The arrows point to the slightly sclerotised bugle at the base of the fangs. Scale bars: A–G = 0.5 mm; H = 0.2 mm.

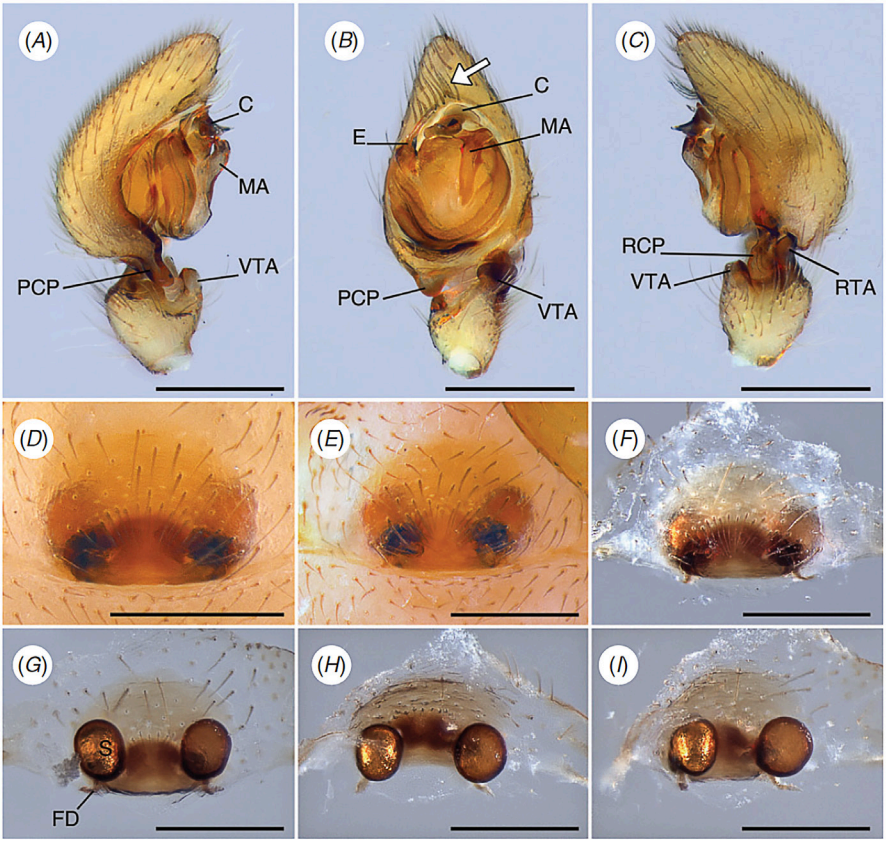

Fig. 13. *Suffascar albolineatus*, gen. et sp. nov., genitalia. (*A*) Male holotype, palp, prolateral view. (*B*) As previous, ventral view. The arrow points to the modified ventral setae. (*C*) As previous, retrolateral view. (*D*) Female paratype (CASENT 9031095), epigyne, ventral view. (*E*) As previous, other female from the same vial. (*F*) As previous, cleared. (*G*) As previous, dorsal view. (*H*) As previous, slightly anterior view. (*I*) As previous, dorso-lateral view. C: conductor; E: embolus; FD: fertilisation duct; MA: median apophysis; PCP: prolateral cymbial process; RCP: retrolateral cymbial process; RTA: retrolateral tibial apophysis; S: spermatheca; VTA: ventral tibial apophysis. Scale bars = 0.2 mm.

Female (paratype collected with holotype)

Total length 2.54; carapace 1.25 long, 0.84 high, 0.57 wide, narrowed to 0.72 in eye region.

Colour (Fig. 12*C–G*). Very similar to male; dorsum of abdomen somewhat darker and median white stripe narrower and more defined.

Epigyne (Figs 13*D–I*, 14*C*). Oval area with longest axis transverse; entrance openings near posterior rim; dark spermathecae and paler bladders visible in transparency; bladders close together, smaller than spermathecae.

Variation

In both sexes, the pattern of the abdomen is variable, with more-or-less contrasting median pale line; in females, the entrance ducts, spermathecae and bladders may be less visible than in the described specimen.

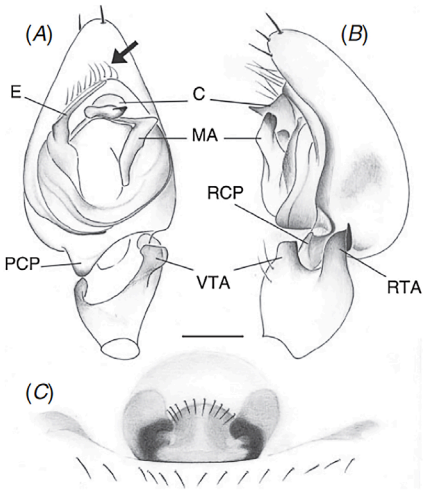

Fig. 14. *Suffascar albolineatus*, gen. et sp. nov., drawings of genitalia. (*A*) Male holotype, palp, ventral view. The arrow points to the modified ventral setae. (*B*) As previous, retrolateral view. (*C*) Female paratype (CASENT 9031095), epigyne, ventral view. C: conductor; E: embolus; MA: median apophysis; PCP: prolateral cymbial process; RCP: retrolateral cymbial process; RTA: retrolateral tibial apophysis; VTA: ventral tibial apophysis. Scale bar = 0.1 mm.

Distribution

S. albolineatus is known from the Ranomafana National Park and vicinity (Fig. 38*B*).

Etymology

The species name refers to the median white line on the abdomen.

Suffascar fianara, sp. nov.

(Figs 5*A–C*, *E–I*, 6*C–D*, 7*B–E*, 8*A–I*, 9*A–D*, 10*A–D*, 11*A–C*, 15*A–B*, 16*A–E*, 17*A*, *B*, 38*C*)

http://zoobank.org/urn:lsid:zoobank.org:act:1C218680-7C92-41EF-B6F8-39A04FA1AB13

Material examined

Holotype. MADAGASCAR: Fianarantsoa Province: ♂, P.N. Ranomafana, Vohiparara, 21°24.032′S, 47°39.399′E, 1150 m asl, 2–22.i.2001, D.H. & K.M. Kavanaugh, R.L. Brett, E. Elsom & F. Vargas (CASENT 9003473).

Paratypes. **MADAGASCAR**: Fianarantsoa Province: 82 ♂, collected with holotype (CASENT 9003473) (4 ♂ in MRAC 245343); 1 ♂, P. N. Ranomafana, Vohiparara, 3.5 km W Ranomafana, 21°14.243′S, 47°23.842′E, 1150 m asl, 13–14.i.2009, sifting leaf litter, primary montane rainforest, C. Griswold, A. Saucedo & H. Wood (MRAC 245352, ex. CASENT 9030180; DNA Z302); 1 ♀, general collecting day and night, further as previous (MRAC 245353, ex. CASENT 9031230; DNA Z304).

Diagnosis

The male of *S. fianara* is recognised by the shape of the retrolateral tibial apophysis and of the embolus (Figs 9*A–C*, 16*B*, 17*A*). The female is characterised by the epigyne with equilateral triangular central plate, the distal top flanked by large entrance openings, and by the large membranous bladders (Figs 10*A–C*, 16*D*, *E*).

Description

Male (holotype)

Total length 1.92; carapace 1.07 long, 0.58 high, 0.78 wide, narrowed to 0.56 in eye region.

Colour (Fig. 15*A–F*). Carapace, chelicerae and sternum uniform reddish brown; dark oval area in front of AME and dark rings around all eyes except PME, which have dark triangle in front of each. Legs pale yellow, coxae slightly darker. Abdomen: dorsum dark grey with longitudinal pale median stripe; venter and sides pale.

Carapace (Fig. 15*C*, *D*, *F*). Cephalic area smooth, thoracic area reticulate; cervical grooves slightly marked.

Eyes. AME: 0.12; ALE: 0.08; AME–AME: 0.03; AME–ALE: 0.03; PME: 0.03: PLE: 0.08; PME–PME: 0.08; PME–PLE: 0.08.

Clypeus. 0.12, 1.5 × width of ALE. Chilum poorly defined.

Sternum (Fig. 15*E*). Granulate, shield-shaped, 0.59 long, 0.53 wide.

Legs. Tarsus I slightly fusiform.

Spination. All femora with one dorsal spine; metatarsus II with three, metatarsus III and IV with four distal ventral spines.

Leg measurements. Femur: I 0.74, II 0.69, III 0.61, IV 0.81; patella: I 0.25, II 0.26, III 0.28, IV 0.33; tibia: I 0.74, II 0.52, III 0.44, IV 0.69; metatarsus: I 0.59, II 0.57, III 0.54, IV 0.82; tarsus: I 0.54, II 0.44, III 0.33, IV 0.56; Total: I 2.85, II 2.49, III 2.20, IV 3.21.

Male palp (Figs 9*A–D*, 16*A–C*, 17*A*, *B*). Retrolateral tibial apophysis simple, short, parallel-sided, with obliquely truncated tip; cymbium basally with smoothly rounded short prolateral protrusion and large scoop-shaped retrolateral extension, distally with one small spine and ventrally with row of curved setae near rim delimiting bulbus anteriorly; embolus originating on posterior part of rounded tegulum, parallel-sided with tapered tip laterally flattened at both sides; median apophysis strongly curved, sickle-shaped with sharp tip; conductor with sclerotised ventral part and membranous dorsal part forming concavity, accommodating distal part of embolus.

Abdomen. Faint scutum surrounding pedicel, narrow process in centre of dorsum.

Female (paratype CASENT 9031230) (Figs 7*E*, 8*A–I*, 10*A–D*, 11*A–C*)

The only female available was used for molecular analyses and SEM before being described and photographed or drawn.

Epigyne (Figs 10*A–D*, 11*A–C*). Triangular plate with truncated top, entrance ducts close to each other, near anterior rim; bladders large, shaped as 90° sector; spermathecae small, short oval, with large medial pore and dorsal scale like extension.

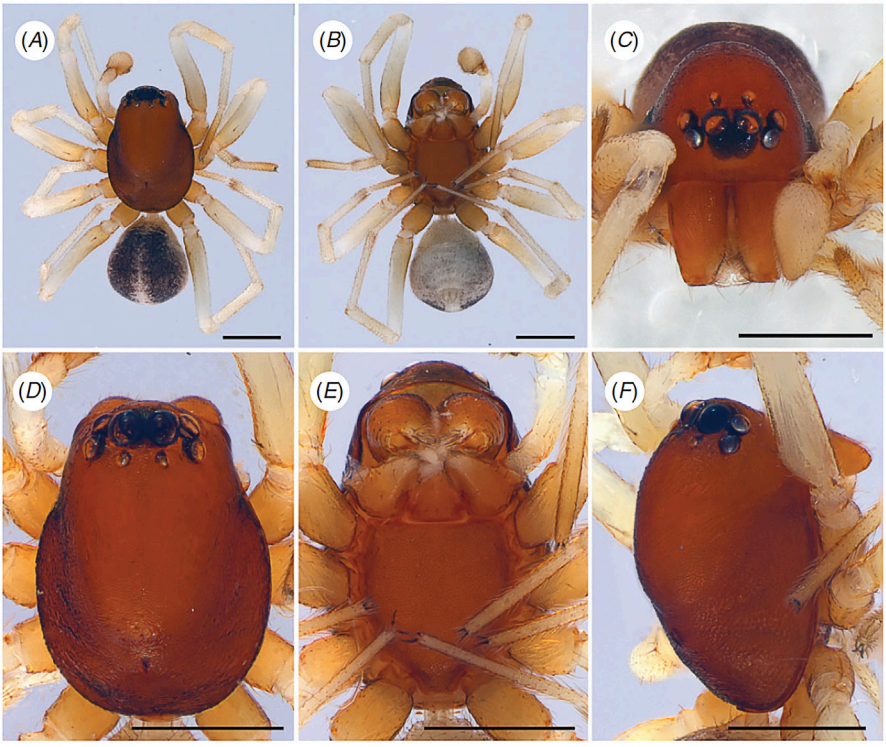

Fig. 15. *Suffascar fianara*, gen. et sp. nov., male holotype. (*A*) Habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, frontal view. (*D*) Carapace, dorsal view. (*E*) As previous, ventral view. (*F*) As previous, lateral view. Scale bars = 0.5 mm.

Variation

The pattern of the male abdomen is variable, it can be much paler than in the holotype and the pale band may be shorter and/or wider, or it can be darker with the scutum much more pronounced and sclerotised.

Distribution

S. fianara is only known from the type locality in the Ranomafana National Park in Madagascar (Fig. 38*C*).

Etymology

The species name is a noun in apposition taken from the first part of the type locality province 'Fianarantsoa'.

Suffascar fisheri, sp. nov.

(Figs 10*E–H*, 18*A–I*, 19*A–H*, 20*A–C*, 38*C*)

http://zoobank.org/urn:lsid:zoobank.org:act:477BC9B8-338D-4341-A066-EE29735D7086

Material examined

Holotype. MADAGASCAR: Fianarantsoa Province: ♂, Réserve Spéciale Ivohibe, 6.5 km ESE Ivohibe, 22°29.8′S, 46°57.3′E, 1575 m asl, 24–30.x.1997, leaf litter, forest, B.L. Fisher (CASENT 9076863).

Paratypes. **MADAGASCAR**: Fianarantsoa Province: 1 ♂, collected with holotype; 6 ♂, 2 ♀, pitfall traps, further as holotype (1 ♀ in MRAC 245354); 1 ♀, Réserve Andringitra, 40 km S Ambalova, 22°13′S, 46°58′E, 1275 m asl, 15.x.1993, pitfall trap rainforest, B.L. Fisher (CASENT 9076864); 2 ♂, 3 ♀, 9 km NE Ivohibe, 22°25.6′S, 46°56.3′E, 900 m asl, 12–17.xi.1997, pitfall traps, forest, B.L. Fisher (CASENT 9076865) (1 ♂, 1 ♀ in MRAC 245355).

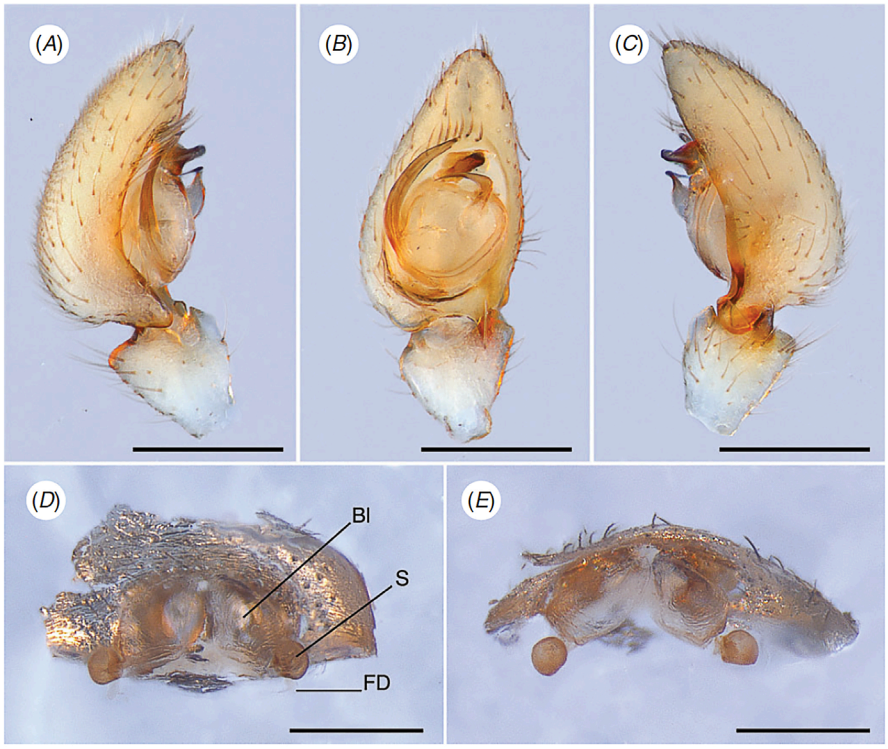

Fig. 16. *Suffascar fianara*, gen. et sp. nov., genitalia. (*A*) Male holotype, palp, prolateral view. (*B*) As previous, ventral view. (*C*) As previous, retrolateral view. (*D*) Female paratype (MRAC 245353, DNA Z304), dried vulva (see the note before the female description for explanation), dorsal view. (*E*) As previous, anterior view. – BI: bladder; FD: fertilization duct; S: spermatheca. Scale bars = 0.2 mm.

Diagnosis

The male of *S. fisheri* is recognised by the broad retrolateral tibial apophysis, the long blade-shaped embolus with deep median fold and the wide median apophysis (Figs 19*B*, *C*, 20*A*, *B*). The female is characterised by the dark, triangular epigyne with a paler base (Fig. 19*D–F*).

Description

Male (holotype)

Total length 1.92; carapace 1.13 long, 0.62 high, 0.76 wide, narrowed to 0.54 in eye region.

Colour (Fig. 18*A–E*). Carapace, chelicerae and sternum uniform pale orange; dark oval area in front of AME and dark rings around all eyes except PME, which have dark triangle in front of them. Legs pale, almost white, tarsus pale orange. Abdomen: dorsum pale grey with ill-defined, paler stripe in anterior part; venter and sides pale.

Carapace (Fig. 18*D*). Cephalic area smooth, thoracic area reticulate; cervical grooves slightly marked.

Eyes. AME: 0.08; ALE: 0.06; AME–AME: 0.03; AME–ALE: 0.02; PME: 0.02: PLE: 0.06; PME–PME: 0.05; PME–PLE: 0.08.

Clypeus. 0.13, 2.2 × width of ALE. Chilum poorly defined.

Sternum. Granulate, shield-shaped, 0.57 long, 0.51 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–III with three distal ventral spines.

Leg measurements. Femur: I 0.69, II 0.64, III 0.57, IV 0.72; patella: I 0.28, II 0.28, III 0.26, IV 0.28; tibia: I 0.56, II 0.44, III 0.39, IV 0.66; metatarsus: I 0.49, II 0.43, III 0.43, IV 0.71; tarsus: I 0.43, II 0.41, III 0.31, IV 0.41; Total: I 2.44, II 2.20, III 1.97, IV 2.77.

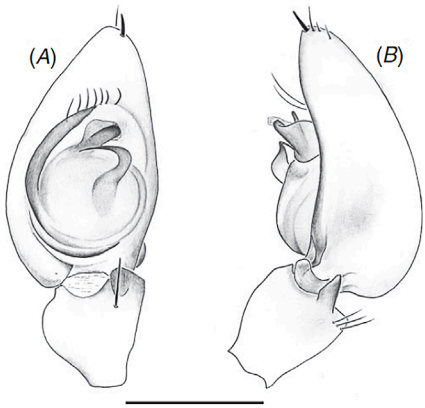

Fig. 17. *Suffascar fianara*, gen. et sp. nov., drawings of male holotype palp. (*A*) Retrolateral view. (*B*) Ventral view. Scale bar = 0.2 mm.

Male palp (Figs 19*A–C*, 20*A*, *B*). Retrolateral tibial apophysis simple, short and broad, parallel-sided, dorsal margin smoothly rounded to obliquely truncated tip; cymbium basally with large sinuous prolateral protrusion and large scoop-shaped retrolateral extension, distally with one small spine and ventrally with row of sinuous setae near rim delimiting bulbus anteriorly; embolus short, originating on prolateral part of rounded tegulum, broad, parallel-sided up to half its length, thence tapered with prolateral side straight, retrolateral side concave, tip blunt; median apophysis broad with anvil-shaped distal part; conductor twice as wide as long with both extremities smoothly rounded; sclerotised ventral part and membranous dorsal part forming concavity, accommodating distal part of embolus.

Female (paratype CASENT 9076864)

Total length 2.39; carapace 1.15 long, 0.63 high, 0.81 wide, narrowed to 0.59 in eye region.

Colour (Fig. 18*F–I*). Very similar to male but legs yellow and with darker tarsus.

Epigyne (Figs 10*E–H*; 19*D–H*, 20*C*). Triangular area, as long as wide, with rounded corners; frontal part dark, posterior part pale, itself darker in the centre. Spermathecae wide apart, oval, with straight median side, provided with three large medial pores in shallow groove, without small, dorsal extension; bladders crumple, larger than spermathecae.

Variation

The pattern of the male abdomen is variable, it can be much paler than in the holotype and the pale band may be shorter and/or wider.

Distribution

S. fisheri is only known from the vicinity of Ivohibe in Madagascar (Fig. 38*C*).

Etymology

The species name is a patronym in honour of Brian Fisher, who collected all known material of the species.

Suffascar fitzpatrickae, sp. nov.

(Figs 21*A–G*, 38*C*)

http://zoobank.org/urn:lsid:zoobank.org:act:49F0D06C-9783-45A6-B3F5-3F7D520F1E21

Material examined

Holotype. MADAGASCAR: Toamasina Province: ♀, Masoala Peninsula, 6.9 km NE Ambanizana, Andranobe, 15°34′S, 50°00′E, 825 m asl, 12.xii.1993, pitfall trap, rainforest, B.L. Fisher, field number 48 (CASENT 9076866).

Diagnosis

The female of *S. fitzpatrickae* is recognised by the two-lobed paler area in front of fovea (Fig. 21*A*) and the epigyne with a rectangular central plate with lateral sides slightly converging towards the front (Fig. 21C–E).

Description

Female (holotype)

Total length 2.91; carapace 1.49 long, 0.78 high, 0.99 wide, narrowed to 0.64 in eye region.

Colour (Fig. 21*A*, *B*). Carapace medium brown with large two-lobed paler area in front of fovea flanked by two tiny dark spots in front; dark oval area in front of AME and dark rings around all eyes except PME, which have dark patch in front of them, not reaching AME; chelicerae and labium medium brown, endites paler; sternum pale yellowish brown; legs pale with metatarsus and tarsus slightly darker yellowish. Abdomen: dorsum grey with broad pale stripe in posterior half; sides and venter white.

Carapace. Entirely smooth; cervical grooves slightly marked.

Eyes. AME: 0.09; ALE: 0.08; AME–AME: 0.02; AME–ALE: 0.03; PME: 0.07: PLE: 0.08; PME–PME: 0.06; PME–PLE: 0.10.

Clypeus. 0.14, 2 × width of ALE. Chilum a single sclerite 0.06 high, 0.15 wide.

Sternum. Shield-shaped, smooth, 0.66 long, 0.62 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine on culminating point at 1/4 of length; metatarsus II with three, metatarsus III and IV with four distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.80, II 0.69, III 0.71, IV 0.98; patella: I 0.34, II 0.30, III 0.33, IV 0.39; tibia: I 0.64, II 0.49, III 0.49, IV 0.74; metatarsus: I 0.64, II 0.54, III 0.64, IV 1.00; tarsus: I 0.46, II 0.39, III 0.39, IV 0.61; Total: I 2.89, II 2.41, III 2.56, IV 3.72.

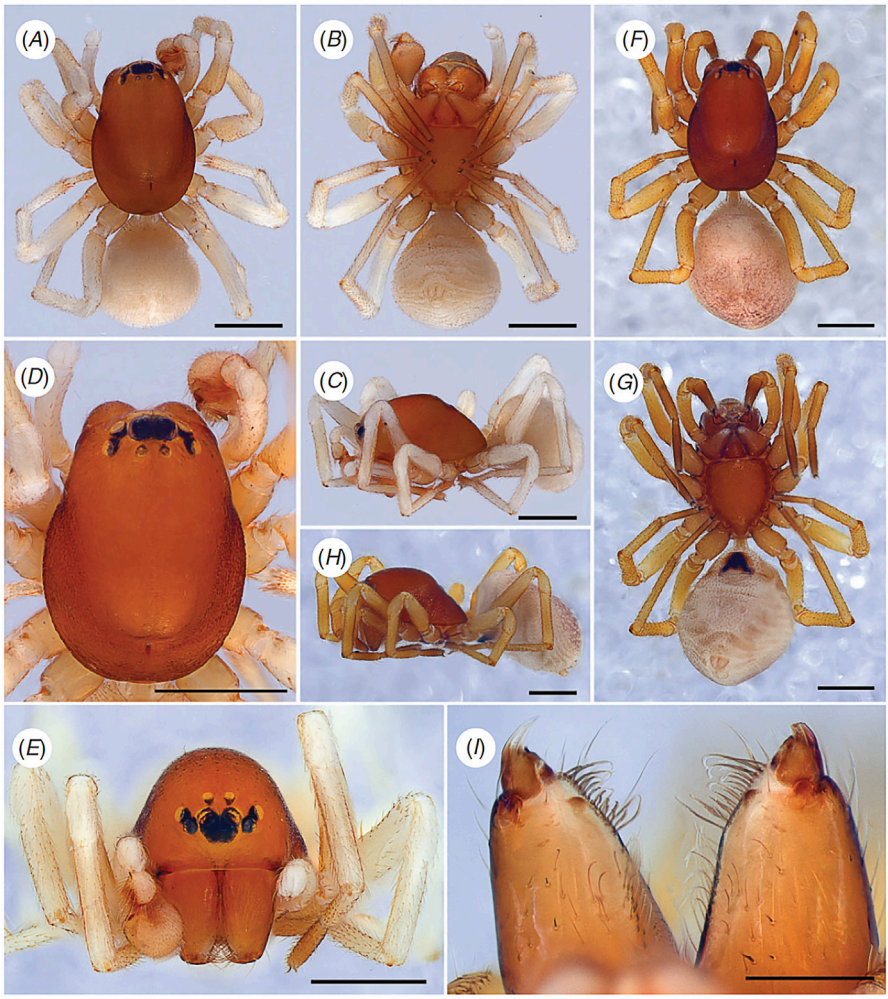

Fig. 18. *Suffascar fisheri*, gen. et sp. nov., (*A*) Male holotype, habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous lateral view. (*D*) As previous, carapace, dorsal view. (*E*) As previous, anterior view. (*F*) Female paratype, habitus, dorsal view. (*G*) As previous, ventral view. (*H*) As previous, lateral view. (*I*) As previous, chelicerae, ventral view. Scale bars: A–H = 0.5 mm; I = 0.2 mm.

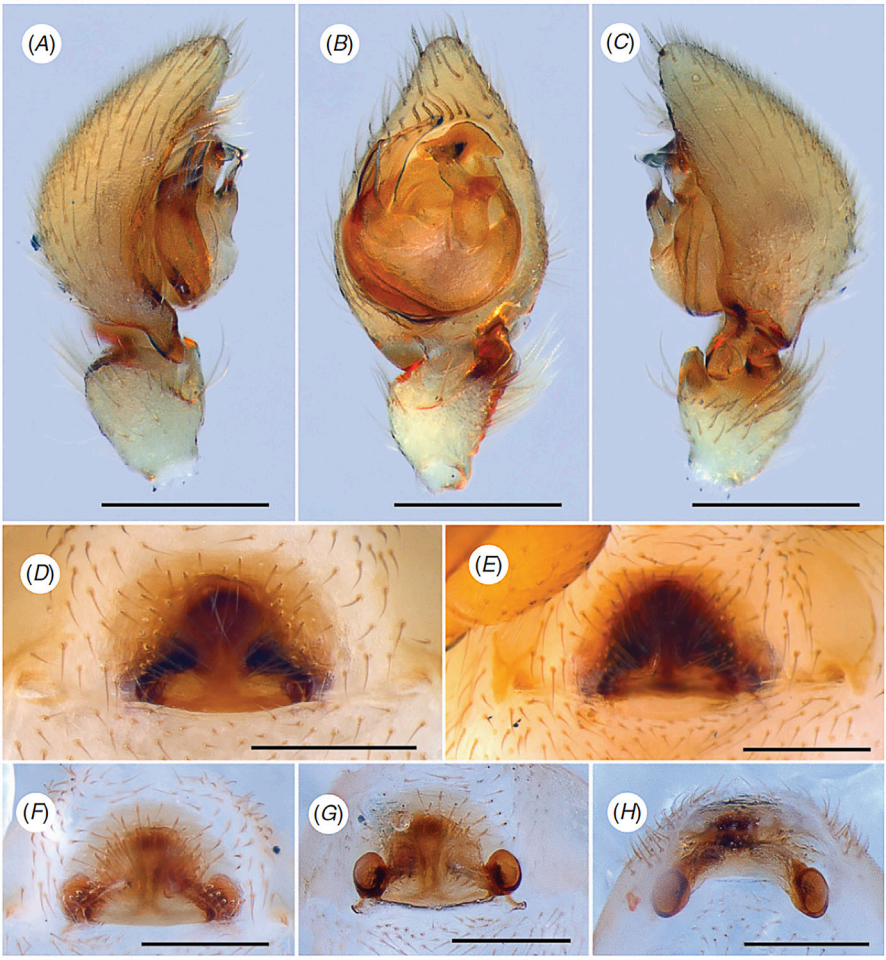

Fig. 19. *Suffascar fisheri*, gen. et sp. nov., genitalia. (*A*) Male holotype, palp, prolateral view. (*B*) As previous, ventral view. (*C*) As previous, retrolateral view. (*D*) Female paratype, epigyne, ventral view. (*E*) As previous, other female. (*F*) As previous, cleared. (*G*) As previous, dorsal view. (*H*) As previous, slightly anterior view. Scale bars = 0.2 mm.

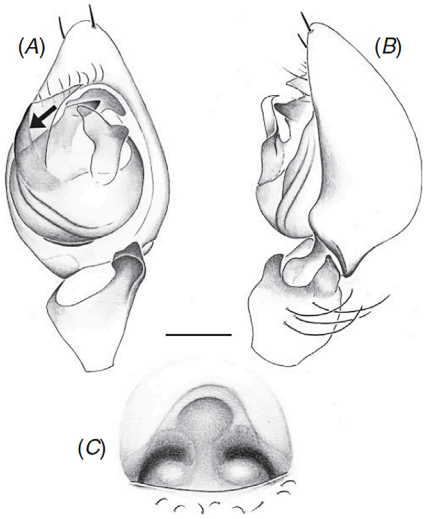

Fig. 20. *Suffascar fisheri*, gen. et sp. nov., drawings of genitalia. (*A*) Male holotype, palp, ventral view. The arrow points to the deep median fold. (*B*) As previous, retrolateral view. (*C*) Female paratype, epigyne, ventral view. Scale bar = 0.1 mm.

Epigyne (Fig. 21*C–G*). An ill-defined orange area with roughly rectangular median plate with sides slightly converging towards the front; laterally with slightly darker patches. Spermathecae, far apart, rounded; copulatory ducts very thin; bladders widely separated, approximately the same size as the spermathecae.

Male

Unknown.

Distribution

S. fitzpatrickae is only known from the type locality in Madagascar (Fig. 38*C*).

Etymology

The species name is a patronym in honour of Moira Fitzpatrick in esteem for her arachnological work and for her important contributions to the conservation of natural history collections in Zimbabwe.

Suffascar gigas, sp. nov.

(Figs 22*A–E*, 23*A–E*, 38*C*)

http://zoobank.org/urn:lsid:zoobank.org:act:AD7A3DFB-9235-4B41-BFFF-9D309E767D60

Material examined

Holotype. MADAGASCAR: Toamasina Province: ♀, Forêt Classée Sandranantitra, 18°2.9′S, 49°5.5′E, 450 m asl, 18–21.i.1999, rainforest, sifted litter, H.J. Ratsirarson (CASENT 9014010).

Diagnosis

The female of *S. gigas* is easily recognised by the shape of the carapace, which is hardly narrowed in front (Fig. 22*A*), the tiny PME, the ALE not touching the AME (Fig. 22*D*) and the elongate labium and endites (Fig. 22*E*).

Description

Female (holotype)

Total length 4.69; carapace 2.27 long, 1.42 high, 1.49 wide, narrowed to 1.35 in eye region.

Colour (Fig. 22*A–E*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes except PME. Legs uniform yellow. Abdomen: uniform pale cream.

Carapace (Fig. 22*A*, *D*). Carapace smooth, subrectangular; cervical grooves absent.

Eyes. AME: 0.12; ALE: 0.10; AME–AME: 0.03; AME–ALE: 0.07; PME: 0.04: PLE: 0.10; PME–PME: 0.07; PME–PLE: 0.18.

Clypeus. 0.20, 2 × width of ALE. Chilum a wide triangle, 0.08 high, 0.49 wide.

Endites and labium. 0.39 wide, 0.57 long; elongate (Fig. 22*E*).

Sternum. Smooth, shield-shaped, 1.07 long, 0.85 wide.

Legs. Tarsus I and II very slightly fusiform.

Spination. All femora with one dorsal spine; metatarsus I with two, II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 1.39, II 1.26, III 1.13, IV 1.53; patella: I 0.52, II 0.51, III 0.49, IV 0.57; tibia: I 1.07, II 0.87, III 0.74, IV 1.15; metatarsus: I 0.98, II 0.85, III 0.84, IV 1.39; tarsus: I 0.82, II 0.66, III 0.64, IV 0. 87; Total: I 4.79, II 4.15, III 3.84, IV 5.51.

Epigyne (Fig. 21*A–E*). Broad, roughly rectangular area, with large spherical spermathecae on extremities visible in transparency; posterior rim with triangular dark area itself with paler semi-circle. Bladders apparently absent.

Male

Unknown.

Distribution

S. gigas is only known from the type locality in Madagascar (Fig. 38*C*).

Remarks

This species is aberrant in many respects. The size, shape of the carapace and the poorly developed bladders in the epigyne all point to the possibility that, despite the cheliceral bugle characteristic of the genus, this species belongs in an as-yet undescribed genus in the dual femoral gland clade.

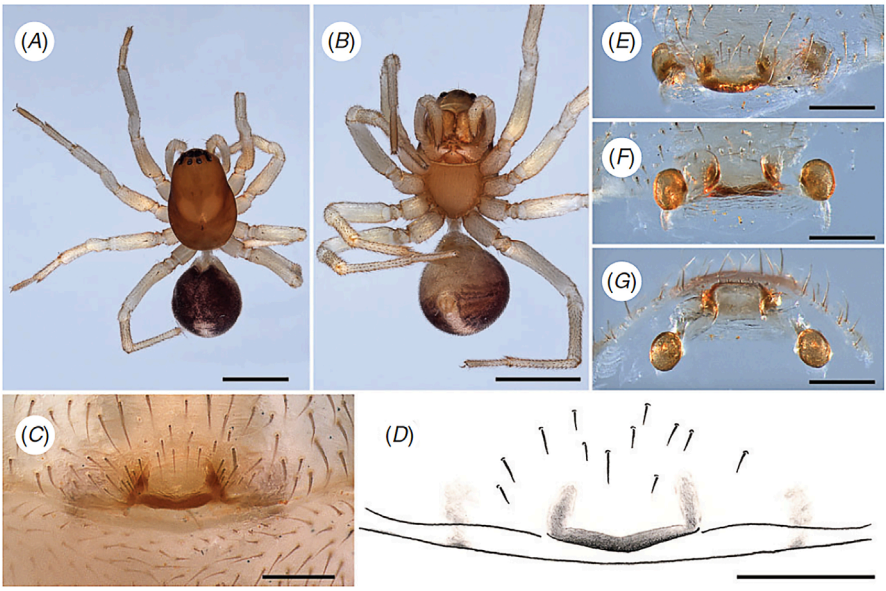

Fig. 21. *Suffascar fitzpatrickae*, gen. et sp. nov., female holotype. (*A*) Habitus, dorsal view. (*B*) As previous, ventral view. (*C*) Epigyne, ventral view. (*D*) As previous, drawing. (*E*) Cleared epigyne, ventral view. (*F*) As previous, dorsal view. (*G*) As previous, antero-dorsal view. Scale bars: A, B = 0.5 mm; C–G = 0.2 mm.

Etymology

The species name, *gigas* (huge), refers to the size of the species as compared with that of the congeners.

***Suffascar griswoldi*, sp. nov.**

(Figs 11*D–F*, 24*A–I*, 25*A–J*, 26*A–C*, 38*B*)

http://zoobank.org/urn:lsid:zoobank.org:act:5840AC2B-BF07-44E9-9363-EE36CD8525E8

Material examined

Holotype. MADAGASCAR: Antananarivo Province: ♂, 3 km 41° NE Andromay, 11.5 km 147°SSE Anjozorobe, 18°28′24″S, 47°57′36″E, 1300 m asl, 15–30.xii.2000, pitfall traps, montane rainforest, Fisher-Griswold Arthropod team BLF2370 (CASENT 9002166).

Paratypes. **MADAGASCAR**: Antananarivo Province: 20 ♀, collected with holotype (2 ♀ in MRAC 245356); 3 ♂, as holotype, BLF2731 (CASENT 9002918) (1 ♂ in MRAC 245357); 10 ♀, general collecting, montane rainforest, Griswold *et al.* BLF2543 further as holotype (CASENT 9004340); 1 ♀, cryptic searching, further as preceding (CASENT 9003022).

Other material examined. **MADAGASCAR**: Toamasina Province: 1 ♂, Parc National Mantadia, 18°47.5′S, 48°25.6′E, 895 m asl, 28.xi–1.xii.1998, sifted litter, H.J. Ratsirarson, #112 (CASENT 9014012); 1 ♂, Forêt Classée Didy, 18°11.9′S, 48°34.7′E, 980 m asl, 18–23.xii.1998 montane rainforest, sifted litter, H.J. Ratsirarson, #131 (CASENT 9006299); 1 ♂, Masoala Peninsula, 6.9 km NE Ambanizana, Andranobe, 15°34′S, 50°00′E, 825 m asl, 12.xii.1993, pitfall trap, rainforest, B.L. Fisher (CASENT 9076867); 1 ♂, 2.xii.1993, sifted litter, leaf mould, rotten wood, rainforest, further as preceding (CASENT 9076868).

Diagnosis

The male of *S. griswoldi* is recognised by the shape of the retrolateral tibial apophysis with tip strongly curved down and the long, sinuous median apophysis with sharp, bent tip (Fig. 25*B*, *C*, 26*A*, *B*). The female is characterised by the epigyne with a subrectangular central plate, its lateral sides slightly diverging anteriorly (Figs 25*D–J*, 26*C*).

Description

Male (holotype)

Total length 2.02; carapace 1.07 long, 0.56 high, 0.76 wide, narrowed to 0.52 in eye region.

Colour (Fig. 24*A–D*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes except PME, which have dark patch in front of them reaching AME. Legs brownish yellow. Abdomen: dorsum pale sepia with broad pale stripe in posterior half; sides pale sepia, venter white.

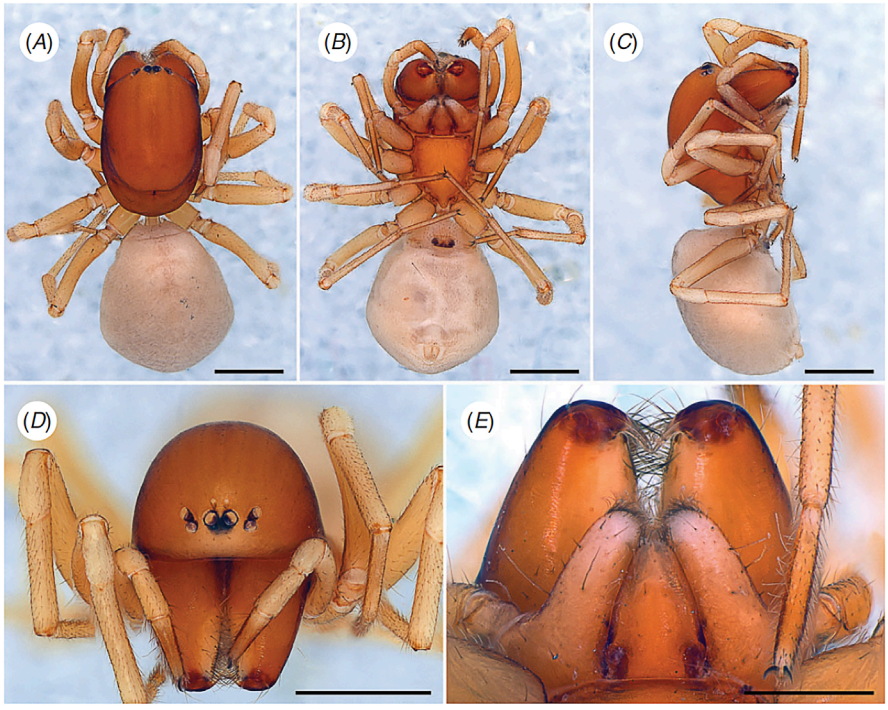

Fig. 22. *Suffascar gigas*, gen. et sp. nov., female holotype. (*A*) Habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, lateral view. (*D*) As previous, anterior view. (*E*) Chelicerae, ventral view. Scale bars: A–D = 1 mm; E = 0.5 mm.

Carapace. Cephalic area smooth, thoracic area reticulate; cervical grooves slightly marked.

Eyes. AME: 0.12; ALE: 0.07; AME–AME: 0.02; AME–ALE: 0.02; PME: 0.05: PLE: 0.07; PME–PME: 0.08; PME–PLE: 0.08.

Clypeus. 0.14, 2 × width of ALE. Chilum triangular.

Sternum. Granulate, shield-shaped, 0.62 long, 0.54 wide, posterior extremity shallowly indented.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine on culminating point at 1/4 of length; metatarsus II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.82, II 0.66, III 0.61, IV 0.82; patella: I 0.26, II 0.25, III 0.25, IV 0.33; tibia: I 0.59, II 0.49, III 0.41, IV 0.51; metatarsus: I 0.57, II 0.39, III 0.49, IV 0.74; tarsus: I 0.52, II 0.33, III 0.43, IV 0.56; Total: I 2.77, II 2.12, III 2.20, IV 2.95.

Male palp (Figs 25*A–C*, 26*A*, *B*). Retrolateral tibial apophysis simple, fairly long and slender, tapered to sharp tip, which is curved down; cymbium basally with prolateral protrusion with rounded extremity and small scoop-shaped retrolateral extension, distally with one small spine and ventrally with row of six modified setae near rim delimiting bulbus anteriorly; embolus fairly long surpassing cymbial rim, originating on prolateral part of rounded tegulum, broad at base, gradually tapered to sharp tip; median apophysis large, sinuous with long distal sclerotised part pointing prolaterad; conductor twice as wide as long with sclerotised ventral part pointing retrolaterad and membranous dorsal part forming concavity.

Female (paratype from CASENT 9002166)

Total length 2.55; carapace 1.28 long, 0.74 high, 0.82 wide, narrowed to 0.50 in eye region.

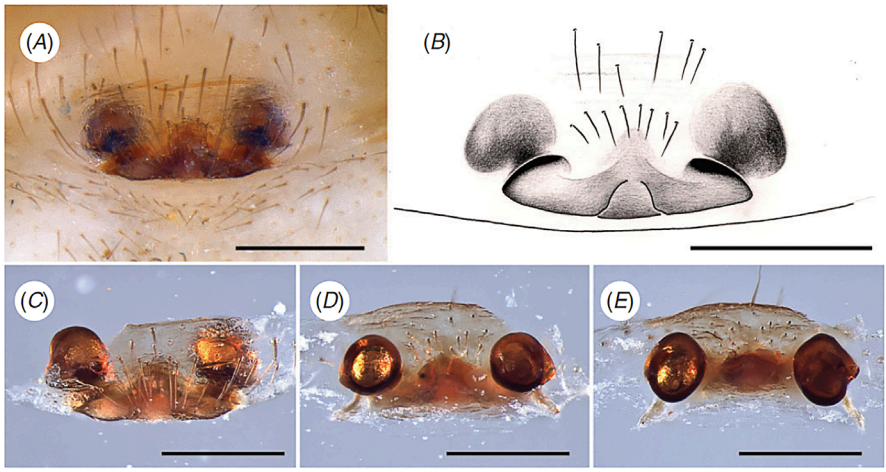

Fig. 23. *Suffascar gigas*, gen. et sp. nov., female holotype, genitalia. (*A*) Epigyne, ventral view. (*B*) As previous, drawing. (*C*) Cleared epigyne, ventral view. (*D*) As previous, dorsal view. (*E*) As previous, antero-dorsal view. Scale bars = 0.2 mm.

Colour. Very similar to male but black patches in front of PME not reaching AME and legs orange.

Epigyne (Figs 11*D–F*, 25*D–J*, 26*C*). An ill-defined orange area with roughly rectangular median plate with sides slightly diverging towards the front; lateral sides on dark patch. Spermathecae small, far apart, rounded; copulatory ducts very thin.

Variation

Pale stripe on abdomen may be indented. Females may be somewhat darker with darker tarsus; the dark patches in the epigyne surrounding the spermathecae may be absent or present on one or on both sides, reinforcing the plug hypothesis.

Distribution

This species has a fairly large distribution in Madagascar (Fig. 38*B*).

Remarks

The genitalia of *S. griswoldi* are similar to those of *S. macromma*. However, these species can be distinguished by the number of spines and in *S. macromma* the relative distance between the eyes is shorter. Furthermore, the AME of *S. macromma* are much larger.

Etymology

The species name is a patronym in honour of Charles Griswold, who organised many collection trips in Madagascar.

Suffascar macromma, sp. nov.

(Figs 5*D*, 6*A*, *B*, 7*A*, *F–H*, 10*I–L*, 11*G–I*, 27*A–I*, 28*A–J*, 29*A–C*, 38*B*)

http://zoobank.org/urn:lsid:zoobank.org:act:08C82132-8EFF-46AC-8B6E-B828E132EE5C

Material examined

Holotype. MADAGASCAR: Toamasina Province: ♂, Foulpointe, 17°40′S, 49°31′E, xi.1994, forest on sandy soil, litter, A. Pauly (MRAC 207060).

Paratypes. **MADAGASCAR**: Toamasina Province: 6 ♂, 6 ♀, Tamatave, Foulpointe, 17°40′S, 49°31′E, xi.1995, forest on sandy soil, yellow plate, A. Pauly (MRAC 205899); 1 ♂, 11.xi.1993, further as preceding (MRAC 205922); 1 ♀, xi.1994, forest on sandy soil, Berlese extraction of litter at base of trees, further as preceding (MRAC 206874); 1 ♀, 10.xi.1993, marsh with *Pandanus*, further as preceding (MRAC 200158); 1 ♂, 2 ♀, 2. xii.1993, forest on sandy soil, litter sieving, further as preceding (MRAC 200376); 1 ♂, 5 ♀, vii.1994, forest on clay, further as preceding (MRAC 201756); 1 ♂, ix.1994, further as preceding (MRAC 202021); 2 ♀, further as preceding (MRAC 206403); 1 ♀, xi.1994, further as preceding (MRAC 213584); 4 ♀, Pont Onibé, 17°39′ S 49°28′E, xii.1993, forest on clay, Berlèse extraction, A. Pauly (MRAC 177964).

Other material examined. **MADAGASCAR**: Toamasina Province: 1 ♂, SF Tampolo, 10 km NNE Fenoarivo, Atn., 17°17′S, 49°26′E, 10 m asl, 4. iv.1997, pitfall trap, littoral forest, B.L. Fisher #1340 (CASENT 9076869); 1 ♂, sifting litter, B.L. Fisher #1342 further as preceding (CASENT 9076870).

Diagnosis

Suffascar macromma is a small species in which the male has very large AME very close to, or touching all the surrounding eyes (Fig. 27*D*, *F*); the male is further recognised by the very short embolus with its length slightly longer than the width of the base

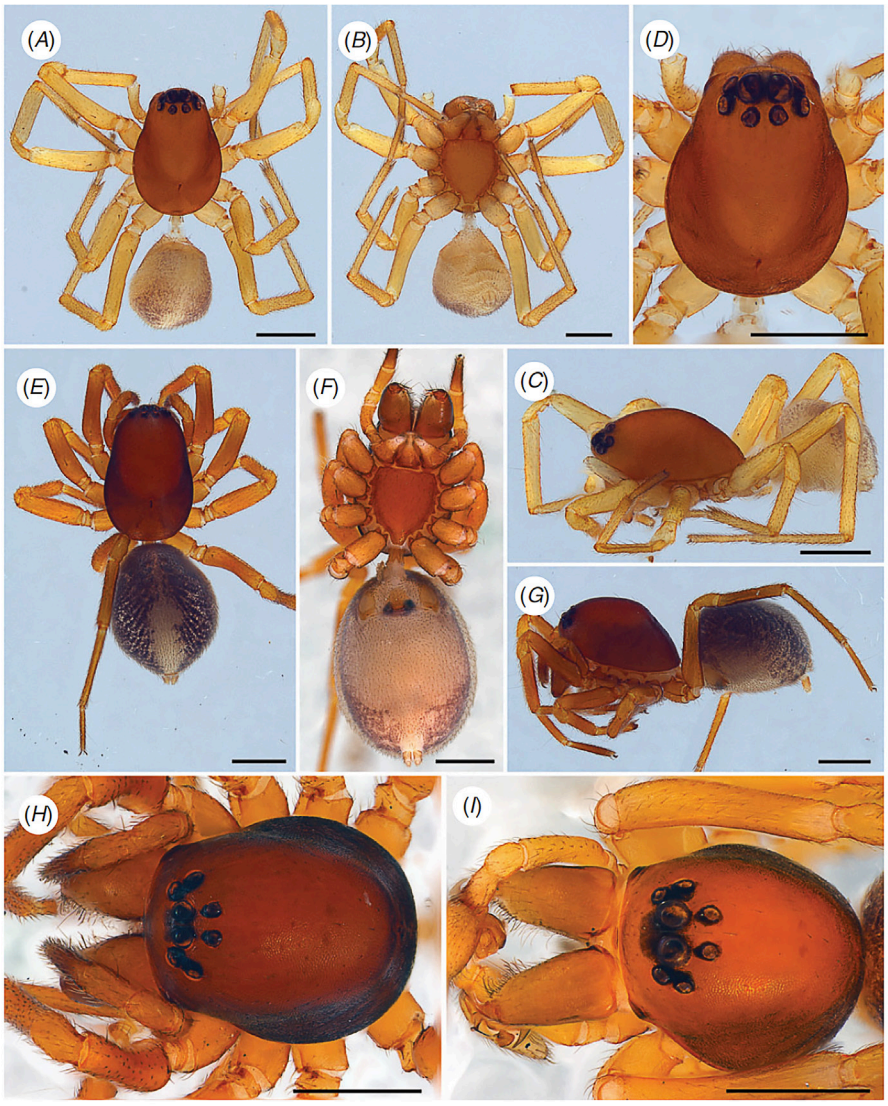

Fig. 24. *Suffascar griswoldi*, gen. et sp. nov. (*A*) Male paratype (CASENT 9006299), habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous lateral view. (*D*) As previous, carapace, dorsal view. (*E*) Female paratype (CASENT 9002166), habitus, dorsal view. (*F*) As previous, ventral view. (*G*) As previous, lateral view. (*H*) As previous, carapace, antero-dorsal view. (*I*) As previous, male holotype. Scale bars = 0.5 mm.

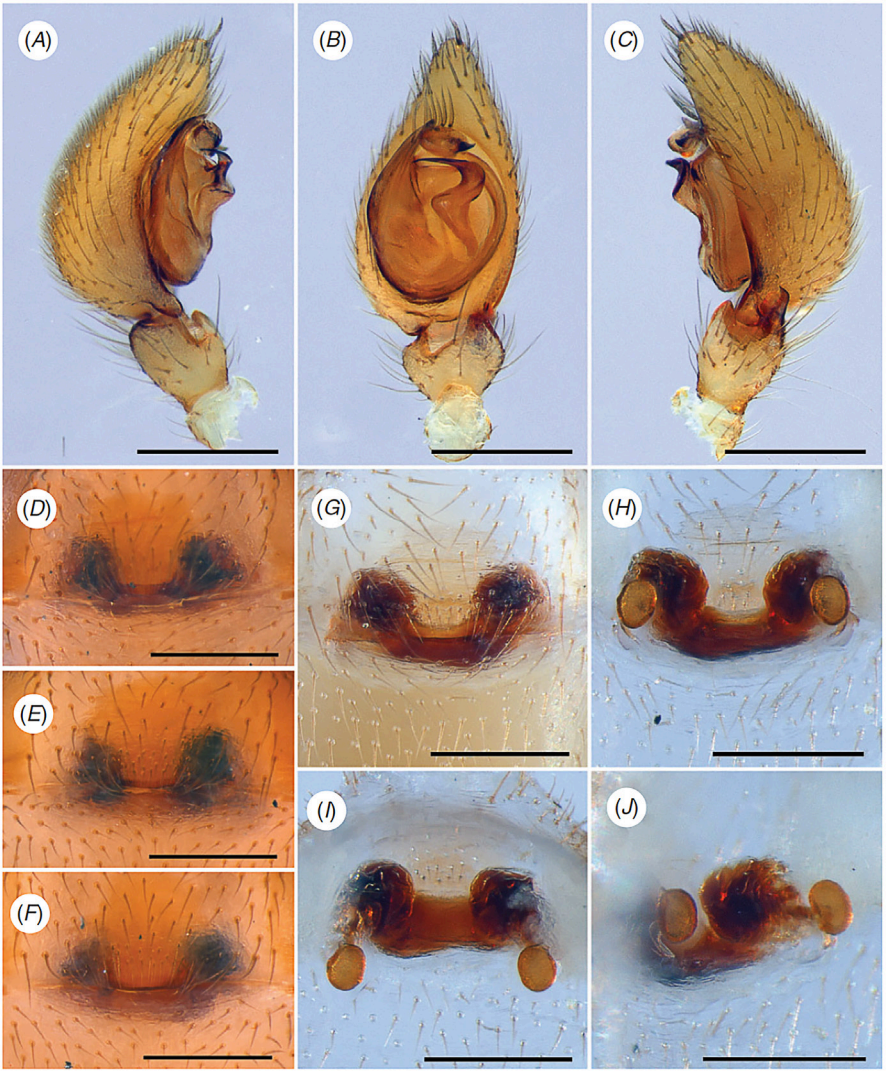

Fig. 25. *Suffascar griswoldi*, gen. et sp. nov., genitalia. (*A*) Male holotype, palp, prolateral view. (*B*) As previous, ventral view. (*C*) As previous, retrolateral view. (*D*) Female paratype (CASENT 9002166), epigyne, ventral view. (*E*) As previous, other female from the same vial. (*F*) As previous, other female from the same vial. (*G*) As previous, cleared. (*H*) As previous, dorsal view. (*I*) As previous, slightly anterior view. (*J*) As previous, dorso-lateral view. Scale bars = 0.2 mm.

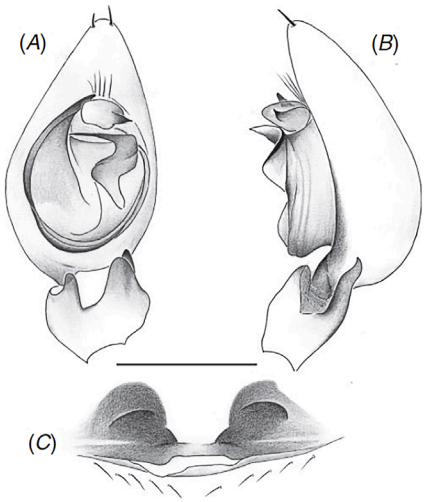

Fig. 26. *Suffascar griswoldi*, gen. et sp. nov., drawings of genitalia. (*A*) Male holotype, palp, ventral view. (*B*) As previous, retrolateral view. (*C*) Female paratype, epigyne, ventral view. Scale bar = 0.2 mm.

and the S-shaped median apophysis (Figs 28*B*, *C*, 29*A*, *B*). The female is characterised by the PME almost touching the AME (Figs 27G, H) and by the simple rounded epigyne with transverse opening (Figs 28*D–G*, 29*C*).

Description

Male (holotype)

Total length 1.55; carapace 0.86 long, 0.46 high, 0.59 wide, narrowed to 0.46 in eye region.

Colour (Fig. 27*A–F*). Carapace, chelicerae and sternum uniform pale orange; dark oval area in front of AME and dark rings around all eyes except PME, which have dark patch touching AME in front of them. Legs brownish yellow. Abdomen: uniform pale grey all over.

Carapace. Cephalic area smooth, thoracic area reticulate; cervical grooves slightly marked.

Eyes. AME: 0.12; ALE: 0.05; AME–AME: 0.02; AME–ALE: 0.00; PME: 0.05: PLE: 0.07; PME–PME: 0.08; PME–PLE: 0.07.

Clypeus. 0.10, 2 × width of ALE. Chilum well defined, triangular.

Sternum. Granulate, shield-shaped, 0.48 long, 0.44 wide, posterior extremity shallowly indented.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II with three, metatarsus III with four and metatarsus IV with two distal ventral spines.

Leg measurements. Femur: I 0.62, II 0.49, III 0.49, IV 0.66; patella: I 0.25, II 0.26, III 0.20, IV 0.25; tibia: I 0.51, II 0.36, III 0.33, IV 0.54; metatarsus: I 0.49, II 0.38, III 0.41, IV 0.57; tarsus: I 0.36, II 0.30, III 0.31, IV 0.44; Total: I 2.23, II 1.79, III 1.74, IV 2.46.

Male palp (Figs 28*A–C*, 29*A*, *B*). Retrolateral tibial apophysis simple, short, triangular with sharp tip curved down; cymbium basally with rounded prolateral protrusion and scoop-shaped retrolateral extension, distally with two small spines and ventrally with row of flattened setae near rim delimiting bulbus anteriorly; embolus very short, almost as wide at base as long; median apophysis broad, S-shaped; conductor with longitudinal ventral part with sclerotised tip and dorsal transverse membranous part, forming concavity.

Female (paratype MRAC 205899)

Total length 1.80; carapace 0.93 long, 0.47 high, 0.61 wide, narrowed to 0.39 in eye region (Fig. 5*D*).

Colour (Figs 29*G–I*). Very similar to male but abdomen with median stripe.

Epigyne (Figs 10*J–L*, 11*G–I*, 28*D–F*, 29*C*). An ill-defined rounded area with transverse opening with recurved extremities near posterior rim; widely separated spermathecae visible in transparency; area around spermathecae darkened but asymmetrical. Spermathecae small, globular, deep in epigyne, far apart; tiny copulatory ducts leading to bladders, which are filled with dark matter, possibly plugs.

Variation

No variation in colour pattern. The epigyne is very variable in that the darkened area may be restricted to one side or extended to both.

Distribution

S. macromma is known from coastal forest in Toamasina Province, Madagascar (Fig. 38*B*).

Remarks

Genitalia of *S. macromma* are similar to those of *S. griswoldi*. However, they can be distinguished by the number of spines and, in *S. macromma*, the relative distance between the eyes is shorter. Furthermore, the AME of *S. macromma* are much larger.

Etymology

The species name, *macromma* (large eyes), a noun in apposition, refers to the size of the AME in the male.

Suffascar micromma, sp. nov.

(Figs 30*A–K*, 38*B*)

http://zoobank.org/um:lsid:zoobank.org:act:B76FF939-CC32-42BA-9201-7C6DEF80D392

Material examined

Holotype. MADAGASCAR: Toamasina Province: ♀, P.N. Mantadia, 18°47.5′S, 48°25.6′E, 895 m asl, 28.xi–I.xii.1998, sifted litter, rainforest, H. J. Ratsirarson #1132 (CASENT 9014017).

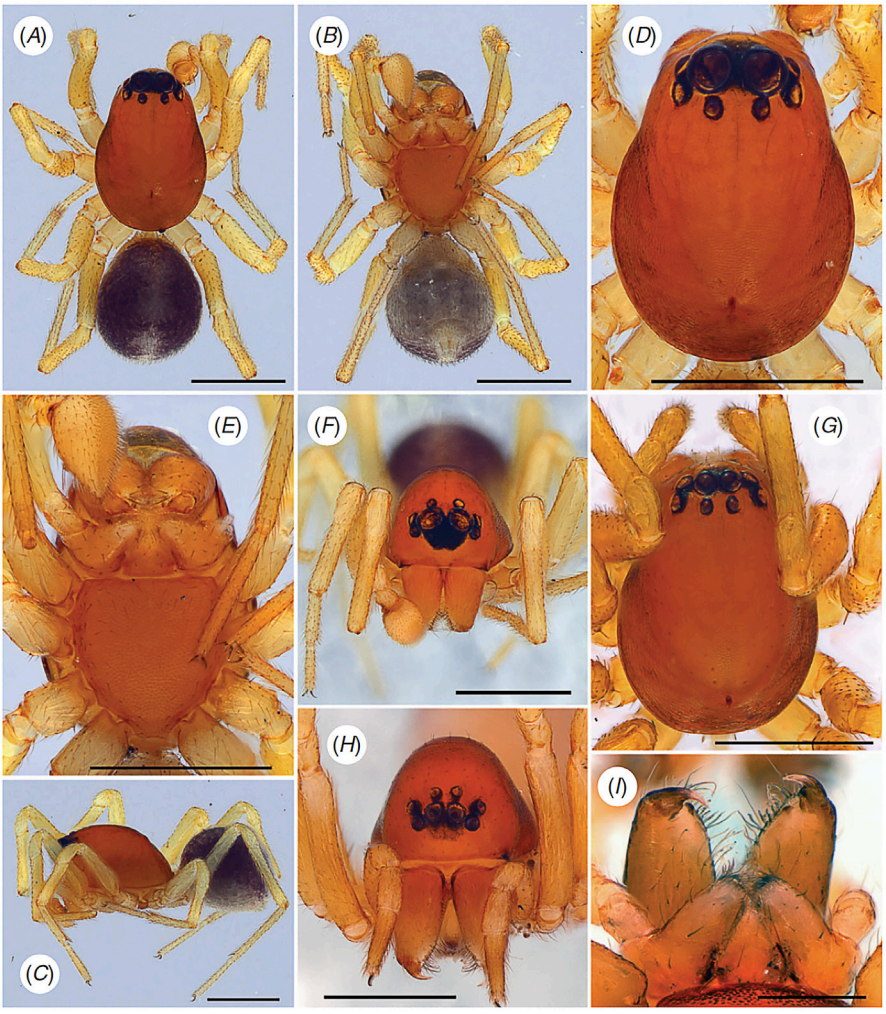

Fig. 27. *Suffascar macromma*, gen. et sp. nov. (*A*) Male (CASENT 9076869), habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous lateral view. (*D*) As previous, carapace, dorsal view. (*E*) As previous, ventral view. (*F*) As previous, frontal view. (*G*) Female paratype (MRAC 205899), carapace, dorsal view. (*H*) As previous, frontal view. (*I*) Male paratype (MRAC 205899). Scale bars: A–H = 0.5 mm; I = 0.2 mm.

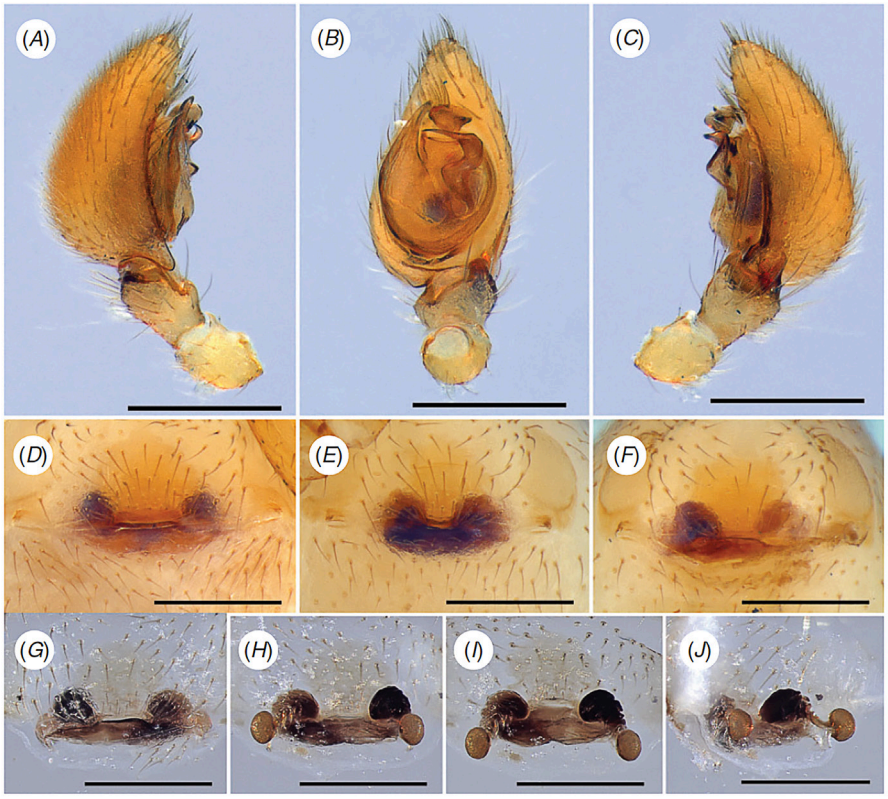

Fig. 28. *Suffascar macromma*, gen. et sp. nov., genitalia. (*A*) Male holotype, palp, prolateral view. (*B*) As previous, ventral view. (*C*) As previous, retrolateral view. (*D*) Female paratype (MRAC 205899), epigyne, ventral view. (*E*) As previous, other female from the same vial. (*F*) As previous, other female from the same vial. (*G*) As previous, cleared. (*H*) As previous, dorsal view. (*I*) As previous, slightly anterior view. (*J*) As previous, dorso-lateral view. Scale bars = 0.2 mm.

Paratype. **MADAGASCAR**: Antananarivo Province: 1 ♀, Réserve speciale d'Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE Ankazobe, 18°30′31″S, 47°17′13″E, 1410 m asl, 17–22.iv.2001, EB09, sifted litter, montane forest, Fisher & Griswold *et al*. (CASENT 9004599).

Diagnosis

Females of *S. micromma* can be recognised by the small PME, the ALE not touching the AME (Fig. 30*D*) and by the epigyne with widely separated, spherical spermathecae at a distance from the epigastric fold (Figs 30*E–K*).

Description

Female (holotype)

Total length 2.137; carapace 1.23 long, 0.71 high, 0.80 wide, narrowed to 0.59 in eye region.

Colour (Figs 30*A–D*). Carapace, chelicerae and sternum uniform yellowish orange; dark oval area in front of AME and dark rings around all eyes except PME, which have small dark spot in front of them. Legs pale yellow, tarsus slightly darker Abdomen: dorsum suffused with sepia on lateral parts of dorsum, sides and venter pale cream.

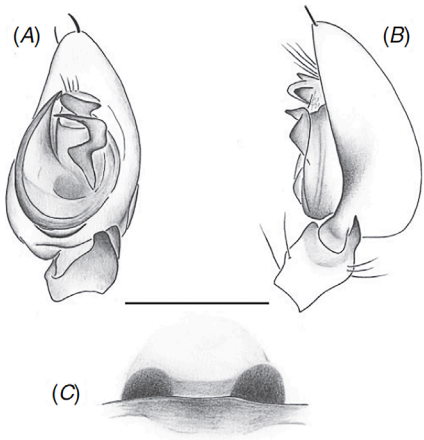

Fig. 29. *Suffascar macromma*, gen. et sp. nov., drawings of genitalia. (*A*) Male holotype, palp, ventral view. (*B*) As previous, retrolateral view. (*C*) Female paratype (MRAC 205899), epigyne, ventral view. Scale bar = 0.2 mm.

Carapace. Carapace slightly reticulated; cervical grooves poorly marked.

Eyes. AME: 0.07; ALE: 0.05; AME–AME: 0.02; AME–ALE: 0.02; PME: 0.03: PLE: 0.05; PME–PME: 0.03; PME–PLE: 0.08.

Clypeus. 0.08, 2.6 × width of ALE. Chilum triangular, slightly wider than long.

Sternum. Slightly reticulated, shield-shaped, 0.61 long, 0.53 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.66, II 0.61, III 0.49, IV 0.74; patella: I 0.30, II 0.25, III 0.25, IV 0.30; tibia: I 0.56, II 0.38, III 0.39, IV 0.64; metatarsus: I 0.49, II 0.48, III 0.49, IV 0.74; tarsus: I 0.48, II 0.43, III 0.33, IV 0.44; Total: I 2.48, II 2.13, III 1.95, IV 2.85.

Epigyne (Fig. 30*E–K*). Roughly rectangular, slightly wider in front than behind; posterior margin with small triangular patch. Spermathecae at a distance from anterior margin, fairly large, spherical, far apart. Bladders small and faint.

Male

Unknown.

Distribution

S. micromma is known from two localities, in Toamasina and Antananarivo Provinces, that are ~25 km apart (Fig. 38*B*).

Etymology

The species name, *micromma*, a noun in apposition, refers to the small PME.

Suffascar nonus, sp. nov.

(Figs 31*A*¬*J*, 38*B*)

http://zoobank.org/urn:lsid:zoobank.org:act:1C8440FE-E21B-4136-A26D-0E60CA581B08

Material examined

Holotype. MADAGASCAR: Antsiranana Province: ♀, Réserve Spéciale d'Anjanaharibe-Sud, 9.2 km WSW Befingotra, 14°45′S, 49°28′E, 1200 m asl, 9.xi.1994, leaf mould, rotten wood, montane rainforest, B. L. Fisher (CASENT 9076871).

Diagnosis

The female of *S. nonus* can be recognised by the epigyne with slightly procurved posterior rim and with two large converging, darker areas, less than their diameter apart (Fig. 31*F*¬*J*).

Description

Female (holotype)

Total length 2.56; carapace 1.35 long, 0.69 high, 0.90 wide, narrowed to 0.49 in eye region.

Colour (Fig. 31*A–E*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes except PME, which have small dark spot in front of them. Legs yellowish orange, tarsus orange. Abdomen: dorsum and sides sepia, venter pale cream with circular white area around spinnerets.

Carapace. Carapace pear-shaped, slightly reticulated; cervical grooves marked.

Eyes: AME: 0.10; ALE: 0.08; AME-AME: 0.02; AME-ALE: 0.02; PME: 0.07: PLE: 0.08; PME-PME: 0.06; PME-PLE: 0.07. XXX

Clypeus. 0.15, 1.9 × width of ALE. Chilum a faintly delimited triangle.

Sternum. Slightly reticulated, shield-shaped, 0.62 long, 0.57 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.75, II 0.69, III 0.64, IV 0.85; patella: I 0.33, II 0.33, III 0.34, IV 0.34; tibia: I 0.57, II 0.46, III 0.46, IV 0.69; metatarsus: I 0.54, II 0.49, III 0.57, IV 0.82; tarsus: I 0.49, II 0.39, III 0.34, IV 0.46; Total: I 2.69, II 2.36, III 1.36, IV 3.17.

Epigyne (Fig. 31*F–J*). Roughly quadrangular area with posterior rim slightly procurved; bladders large, converging anteriorly, visible in transparency as two darker areas with irregularly darker surroundings less than their diameter apart. Spermathecae subglobular, small, far apart.

Male

Unknown.

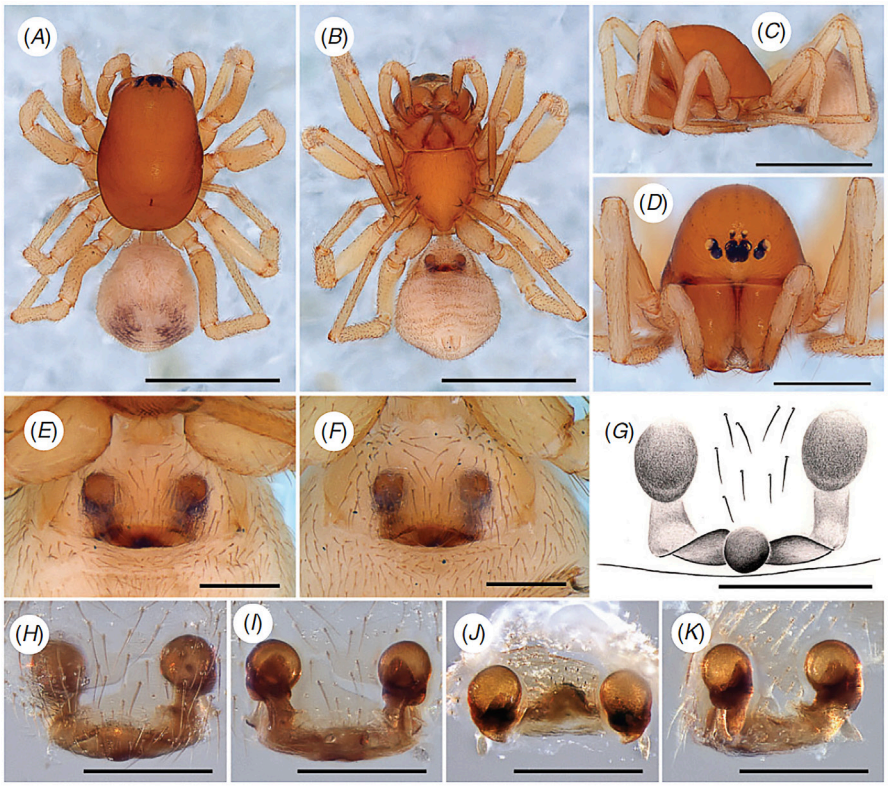

Fig. 30. *Suffascar micromma*, gen. et sp. nov. (*A*) Female holotype, habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, lateral view. (*D*) As previous, frontal view. (*E*) Female holotype, epigyne, ventral view. (*F*) As previous, other female (CASENT 9004599). (*G*) As previous, drawing. (*H*) Female holotype, cleared epigyne, ventral view. (*I*) As previous, dorsal view. (*J*) As previous, antero-dorsal view. (*K*) As previous, dorso-lateral view. Scale bars: A–C = 1 mm; D = 0.5 mm; E–K = 0.2 mm.

Distribution

Known only from the type locality Réserve d'Anjanaharibe-Sud. (Fig. 38*B*).

Etymology

This species is the ninth (*nonus*) described in the genus.

***Suffascar scutatus*, sp. nov.**

(Figs 32*A–F*, 33*A*, *B*, 38*D*)

http://zoobank.org/urn:lsid:zoobank.org:act:BCBF0E2E-8830-4BA5-B6AC-7C53310E618C

Material examined

Holotype. MADAGASCAR: Antananarivo Province: ♂, Réserve special d'Ambohitantely, Forêt d'Ambohitantely, 20.9 km 72° NE Ankazobe, 18°30′31″S, 47°17′13″E, 1410 m asl, 17–22.iv.2001, EB10 pitfall trap, montane forest, B.L. Fisher & C. Griswold (CASENT 9007924).

Paratypes. **MADAGASCAR**: Antananarivo Province: 1 ♂, collected with holotype (CASENT 9007924).

Diagnosis

Males of *S. scutatus* are easily recognised by the presence of a small dorsal scutum (Fig. 32*A*) and the long semicircular embolus (Figs 32*D*, 33*A*).

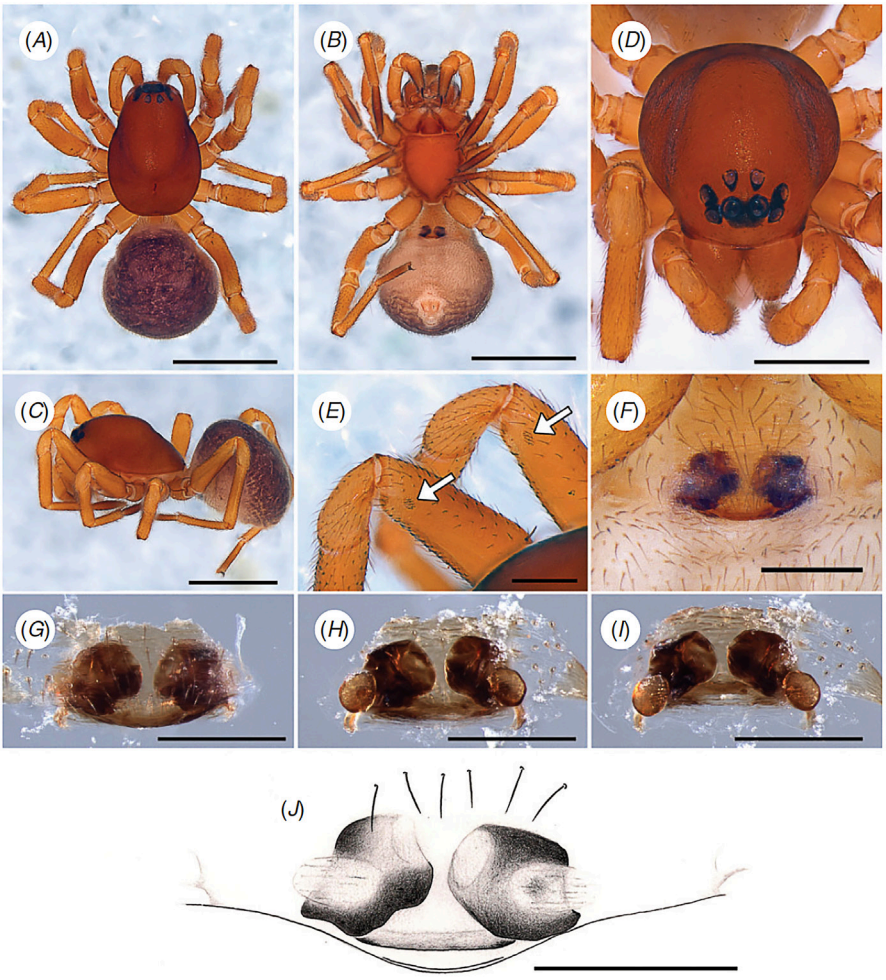

Fig. 31. *Suffascar nonus*, gen. et sp. nov., female holotype. (*A*) Habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, lateral view. (*D*) As previous, carapace, frontal, slightly dorsal view. (*E*) Legs I and II, prolateral view. The arrows show the femoral gland. (*F*) Epigyne, ventral view. (*G*) As previous, cleared. (*H*) As previous, dorsal view. (*I*) As previous, antero-dorsal view. (*J*) As previous, drawing. Scale bars: A–C = 1 mm; D = 0.5 mm; E–J = 0.2 mm.

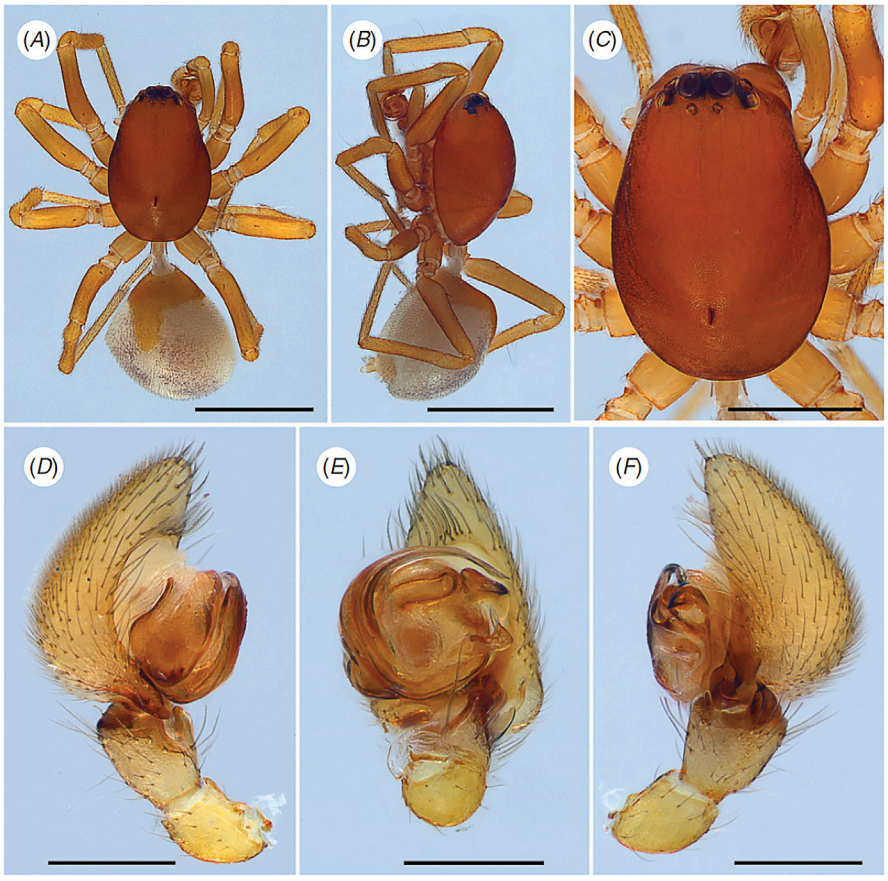

Fig. 32. *Suffascar scutatus*, gen. et sp. nov., male holotype. (*A*) Habitus, dorsal view. (*B*) As previous, lateral view. (*C*) As previous, carapace, dorsal view. (*D*) Palp (expanded: bulbus turned clockwise), prolateral view. (*E*) As previous, ventral view. (*F*) As previous, retrolateral view. Scale bars: A, B = 1 mm; C = 0.5 mm; E–G = 0.2 mm.

Description

Male (holotype)

Total length 2.49; carapace 1.22 long, 0.70 high, 0.82 wide, narrowed to 0.50 in eye region.

Colour (Fig. 32*A–C*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes except PME. Legs yellow. Abdomen: pale, dorsum sparsely suffused with pale sepia apart from central stripe and bright orange scutum.

Carapace. Carapace smooth; cervical grooves faintly marked.

Eyes. AME: 0.10; ALE: 0.08; AME–AME: 0.03; AME–ALE: 0.03; PME: 0.05: PLE: 0.08; PME–PME: 0.07; PME–PLE: 0.10.

Clypeus. 0.12, 1.5 × width of ALE. Chilum absent.

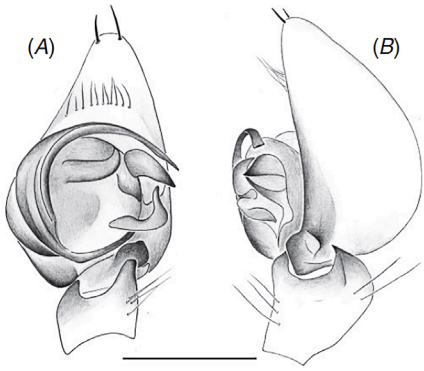

Fig. 33. *Suffascar scutatus*, gen. nov. sp. nov, male holotype, drawings of the palp. (*A*) Ventral view. (*B*) Retrolateral view. Scale bar = 0.2 mm.

Sternum smooth, shield-shaped, 0.62 long, 0.59 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.90, II 0.69, III 0.66, IV 0.90; P: I 0.33, II 0.33, III 0.30, IV 0.36; tibia: I 0.52, II 0.51, III 0.43, IV 0.71; metatarsus: I 0.66, II 0.57, III 0.54, IV 0.85; tarsus: I 0.52, II 0.48, III 0.41, IV 0.57; Total: I 2.94, II 2.57, III 2.33, IV 3.39

Male palp (Figs 32*D–F*, 33*A*, *B*). Retrolateral tibial apophysis fairly large, triangular, pointed, slightly down curved; cymbium basally with prolateral protrusion with blunt tip, and scoop-shaped retrolateral extension, distally with two small spines and ventrally row of about 10 sinuous setae near rim delimiting bulbus anteriorly; embolus long, semicircular, originating on posterior base of rounded tegulum; median apophysis fairly small, rounded distal part with sharp tip pointing forward; conductor with transverse ventral part with sclerotised retrolateral tip and dorsal transverse membranous part, forming concavity.

Abdomen (Fig. 32*A*, *B*). Scutum surrounding pedicel, with narrow extension on posterior part; small scutum around spinnerets.

Female

Unknown.

Distribution

Known only from the type locality Forêt d'Ambohitantely (Fig. 38*D*).

Etymology

The species name, *scutatus*, refers to the presence of a dorsal abdominal scutum in the male.

Suffascar sufficiens, sp. nov.

(Figs 34*A–F*, 35*A–C*, 36*A–C*, 38*D*)

http://zoobank.org/urn:lsid:zoobank.org:act:31000872-C938-4521-B509-8D061CD7A75E

Material examined

Holotype. MADAGASCAR: Antsiranana Province: ♂, Réserve Spéciale d'Anjanaharibe-Sud, 12.2 km WSW Befingotra, 14°45′S, 49°26′E, 1985 m asl, 29.xi.1997, pitfall trap, montane rainforest, B. L. Fisher (CASENT 9076872).

Paratype. MADAGASCAR: ♀, Antsiranana Province: Réserve Spéciale d'Anjanaharibe-Sud, 11.0 km WSW Befingotra, 14°45′S, 49°27′E, 1565 m asl, 16.xi.1994, sifted litter, montane rainforest, B. L. Fisher (CASENT 9076873).

Diagnosis

Males of *S. sufficiens* are similar to those of *S. griswoldi* and *S. macromma* but differ by the shape of the median apophysis, stronger, and the broader retrolateral tibial apophysis (Figs 35*B*, *C*, 36*A*, *B*). Females are recognised by the long palpal claw (Fig. 34*F*) and the widely separated spermathecae and epigynal bladders (Figs 34*G*, 36*C*).

Description

Male (holotype)

Total length 2.37; carapace 1.28 long, 0.70 high, 0.88 wide, narrowed to 0.60 in eye region.

Colour (Fig. 35*A–C*). Carapace, chelicerae and sternum uniform dark orange; dark oval area in front of AME and dark rings around all eyes except PME, which have small dark spot in front of them. Legs yellowish orange, pairs I and II slightly darker with base of femora and tarsus brownish orange. Abdomen: dorsum and sides pale sepia, venter pale.

Carapace. Carapace slightly reticulated.

Eyes. AME: 0.11; ALE: 0.08; AME–AME: 0.02; AME–ALE: 0.01; PME: 0.07: PLE: 0.08; PME–PME: 0.05; PME–PLE: 0.07.

Clypeus. 0.12, 1.5 × width of ALE. Chilum a well delimited triangle as high as wide (Fig. 34*B*).

Sternum. Reticulated, shield-shaped, 0.62 long, 0.59 wide; posterior extremity shallowly indented.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–IV with three distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.98, II 0.75, III 0.71, IV 0.98; patella: I 0.36, II 0.36, III 0.33, IV 0.36; tibia: I 0.77, II 0.48, III 0.56, IV 0.79; metatarsus: I 0.85, II 0.57, III 0.57, IV 0.90; tarsus: I 0.59, II 0.44, III 0.49, IV 0.69; Total: I 3.56, II 2.61, III 2.66, IV 3.72.

Male palp (Figs 35*A–C*, 36*A*, *B*). Retrolateral tibial apophysis simple, short, triangular with sharp tip curved downwards; cymbium basally with rounded prolateral protrusion and scoop-shaped retrolateral extension, distally with two small spines and ventrally with row of flattened setae near rim delimiting bulbus anteriorly; embolus short, slightly longer than wide at base; median apophysis strongly curved, distal part blunt, pointing prolaterad, basal part with prolateral point; conductor transverse, fairly broad.

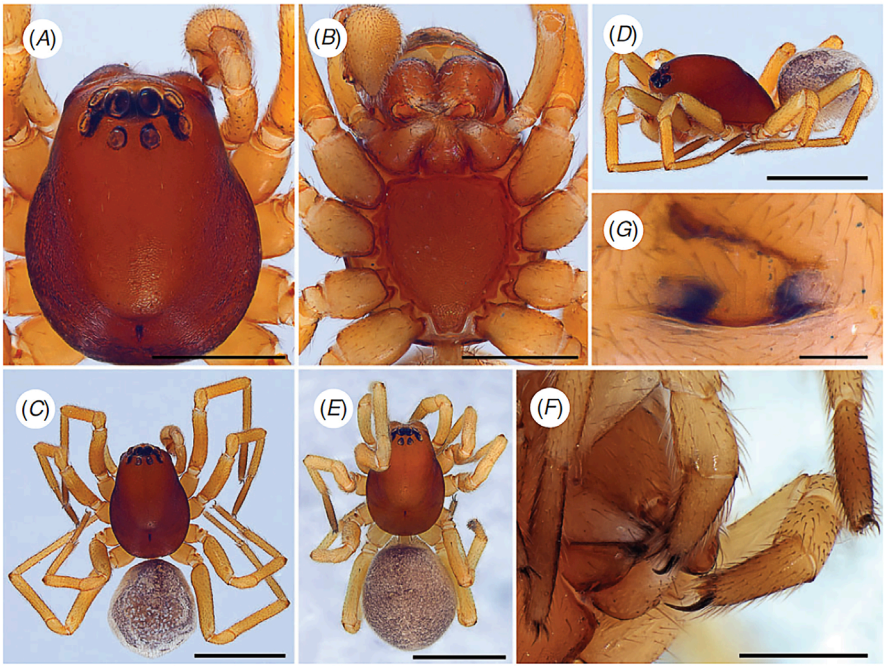

Fig. 34. *Suffascar sufficiens*, gen. et sp. nov. (*A*) Male holotype, carapace, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, habitus, dorsal view. (*D*) As previous, lateral view. (*E*) Female paratype, dorsal view. (*F*) As previous, detail of palpal claws, ventro-lateral view. (*G*) As previous, epigyne, ventral view. Scale bars: A, B = 0.5 mm; C–E = 1 mm; F, G = 0.2 mm.

Female (paratype)

Total length 2.77; carapace 1.42 long, 0.71 high, 0.92 wide, narrowed to 0.50 in eye region.

Colour (Fig. 34*D*, *E*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes. Legs yellow, tarsus orange. Abdomen: dorsum pale grey; sides, venter and spinnerets pale cream.

Carapace. Carapace smooth.

Eyes. AME: 0.08; ALE: 0.08; AME–AME: 0.02; AME–ALE: 0.02; PME: 0.07: PLE: 0.08; PME–PME: 0.05; PME–PLE: 0.07.

Clypeus. 0.13, 1.75 × width of ALE. Chilum triangular, 0.07 high, 0.10 wide.

Sternum. Smooth, shield-shaped, 0.71 long, 0.61 wide, posterior extremity straight.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II–III, with three, metatarsus IV with four distal ventral spines; preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.82, II 0.66, III 0.66, IV 0.89; patella: I 0.34, II 0.34, III 0.34, IV 0.34; tibia: I 0.62, II 0.49, III 0.43, IV 0.72; metatarsus: I 0.56, II 0.52, III 0.54, IV 0.80; tarsus: I 0.44, II 0.41, III 0.38, IV 0.52; Total: I 2.79, II 2.43, III 2.35, IV 3.28.

Palpal claw. Long, almost as long as half the length of tarsus (Fig. 34*F*).

Epigyne (Figs 34*G*, 36*C*). Roughly quadrangular area with posterior rim slightly procurved; spermathecae and bladders visible in transparency as two darker areas with irregularly darker surroundings, slightly more than their diameter apart.

Distribution

Known only from the type locality Réserve d'Anjanaharibe-Sud. (Fig. 38*D*).

Etymology

The species name, *sufficiens* (adequate), refers to the differences with *S. griswoldi* and *S. macromma*, sufficient to recognise the species.

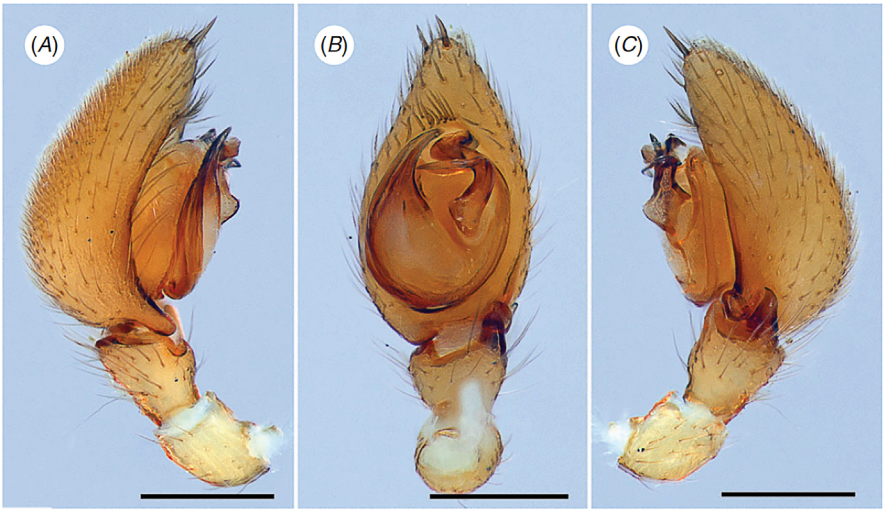

Fig. 35. *Suffascar sufficiens*, gen. et sp. nov., male holotype palp. (*A*) Prolateral view. (*B*) Ventral view. (*C*) Retrolateral view. Scale bar = 0.2 mm.

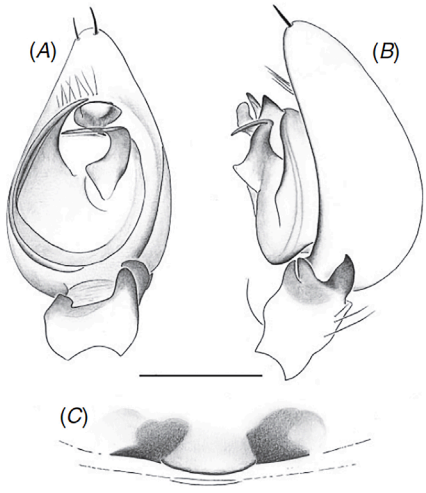

Fig. 36. *Suffascar sufficiens*, gen. et sp. nov., drawings of genitalia. (*A*) Male holotype, palp, ventral view. (*B*) As previous, retrolateral view. (*C*) Female paratype, epigyne, ventral view. Scale bar = 0.2 mm.

Remarks

The sexes were not collected together but occur at the same locality and high altitude, suggesting that they are conspecific. For this reason, the female is tentatively placed with the male. This is why a complete description is given for both sexes.

Suffascar tofti, sp. nov.

(Figs 37*A–F*, 38*D*)

http://zoobank.org/urn:lsid:zoobank.org:act:6661A01A-91E1-4555-A972-706C472735CE

Material examined

Holotype. MADAGASCAR: Toamasina Province: ♀, Forêt Classée Sandranantitra, rainforest, 18°02.9′S, 49°05.5′E, 450 m asl, 21–24.i.1999, sifted litter, H.J. Ratsirarson, #102 (CASENT 9014007).

Diagnosis

The female of *S. tofti* can be recognised by the ALE not touching the AME (Fig. 37*D*) and the epigyne with two large darker areas, separated by a plate with procurved posterior rim, strongly narrowed in front between the spots (Fig. 37*E*, *F*).

Description

Female (holotype)

Total length 2.65; carapace 1.56 long, 0.72 high, 0.91 wide, narrowed to 0.53 in eye region.

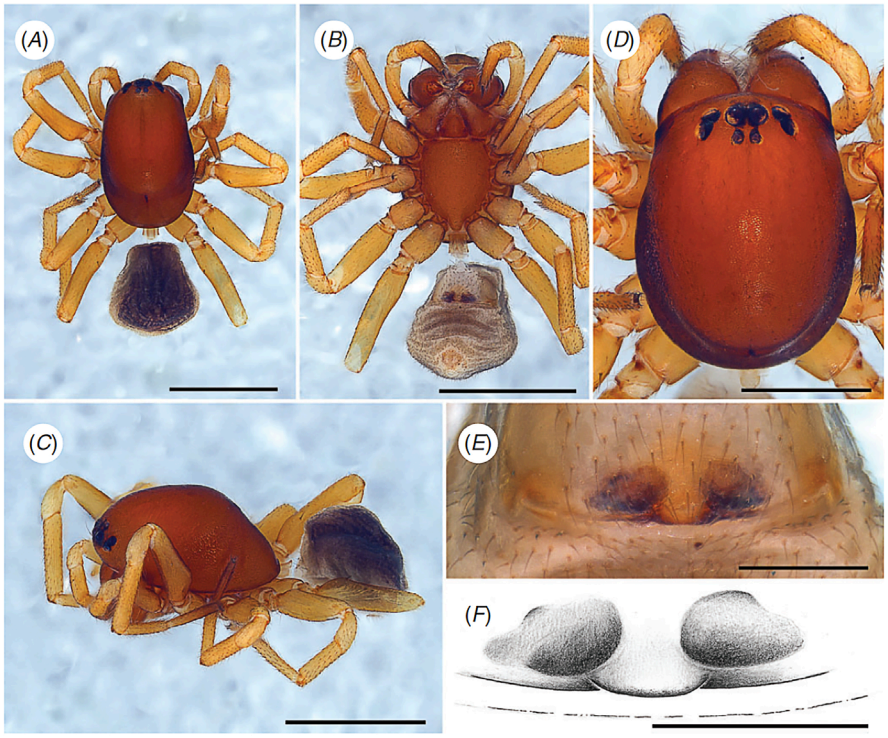

Fig. 37. *Suffascar tofti*, gen. et sp. nov., female holotype. (*A*) Habitus, dorsal view. (*B*) As previous, ventral view. (*C*) As previous, lateral view. (*D*) As previous, carapace, dorsal view. (*E*) Epigyne, ventral view. (*F*) As previous, drawing. Scale bars: A–C = 1 mm; D = 0.5 mm; E, F = 0.2 mm.

Colour (Fig. 37*A–D*). Carapace, chelicerae and sternum uniform orange; dark oval area in front of AME and dark rings around all eyes except PME, which have small dark spot in front of them reaching AME. Legs yellow, tarsus I and II yellowish orange. Abdomen: dorsum pale grey, sides and venter pale cream.

Carapace. Carapace very slightly reticulated.

Eyes. AME: 0.07; ALE: 0.04; AME–AME: 0.03; AME–ALE: 0.03; PME: 0.04: PLE: 0.06; PME–PME: 0.02; PME–PLE: 0.12.

Clypeus. 0.16, 4 × width of ALE. Chilum a faintly delimited triangle, 0.07 high, 0.16 wide.

Sternum. Slightly reticulated, shield-shaped, 0.67 long, 0.57 wide.

Legs. Tarsus I and II fusiform.

Spination. All femora with one dorsal spine; metatarsus II with three, metatarsus III with four distal ventral spines (metatarsus IV lost); preening brushes on metatarsus II and III.

Leg measurements. Femur: I 0.80, II 0.67, III 0.66, IV 0.82; patella: I 0.38, II 0.33, III 0.31, IV 0.33; tibia: I 0.61, II 0.51, III 0.44, IV 0.71; metatarsus: I 0.52, II 0.52, III 0.51, IV lost; tarsus: I 0.44, II 0.39, III 0.38, IV lost; Total: I 2.79, II 2.43, III 2.35.

Epigyne (Fig. 37*E*, *F*). A fairly wide area with two large ovoid spots separated by the narrowed part of a plate with procurved posterior rim.

Male

Unknown.

Distribution

Known only from the type locality Forêt Classée Sandranantitra (Fig. 38*D*).

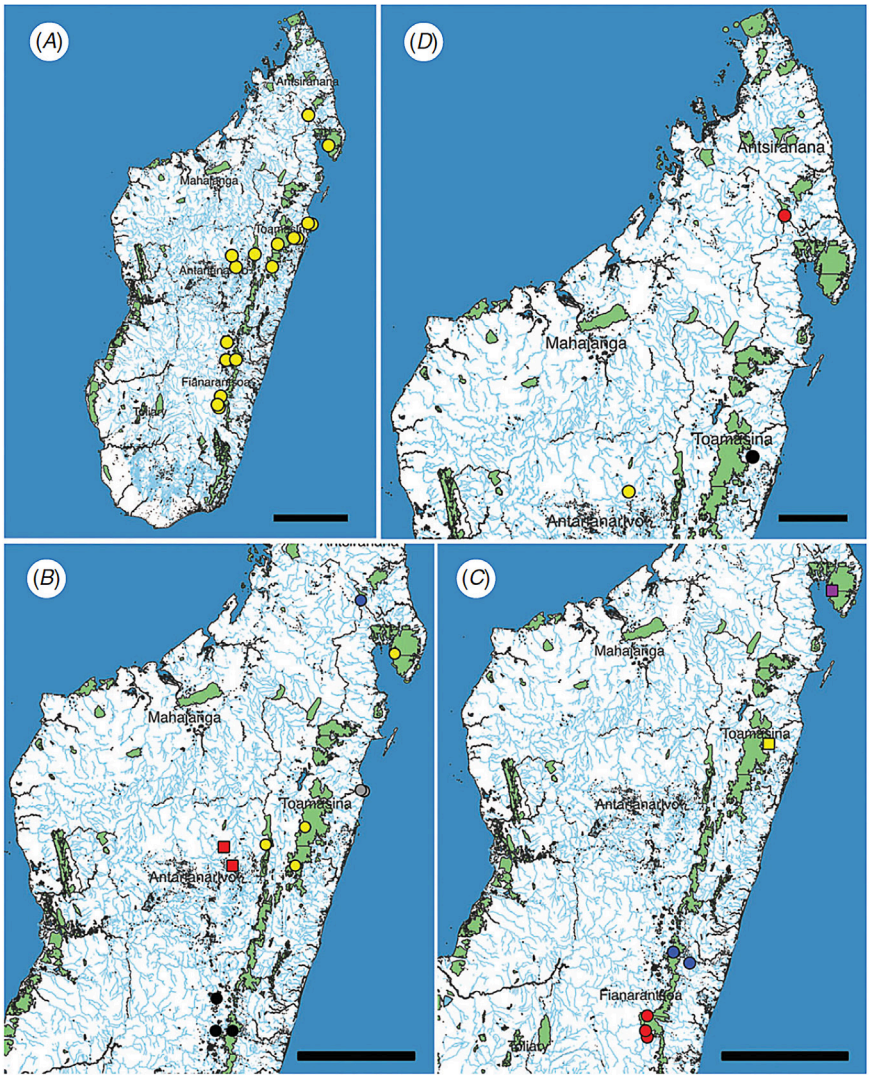

Fig. 38. Distribution map of *Suffascar*, gen. nov. spp. nov. (*A*) Global overview of the distribution of *Suffascar* samples on Madagascar. (*B*) Localities of *S. albolineatus* (black ●), *S. griswoldi* (yellow ●), *S. macromma* (blue ●), *S. micromma* (red ■), *S. nonus* (grey ●), (*C*) Localities of *S. fianara* (blue ●), *S. fisheri* (red ●), *S. fitzpatrickae* (purple ■), *S. gigas* (yellow ■). (*D*) Localities of *S. scutatus* (yellow ●), *S. sufficiens* (red ●) and *S. tofti* (black ●). Scale bars: A–C = 200 km; D = 100 km.

Etymology

The species name is a patronym in honour of Søren Toft in esteem for his ecological work on spiders.

Conclusion

So far, the combined presence of chisel-shaped setae in the preening brush and femoral glands is confirmed in four genera: *Suffasia*, *Asceua*, *Suffrica* and *Suffascar*. This is most probably also the case in *Malayozodarion hoiseni* Ono & Hashim, 2008 (not studied here), which appears closely related to *Suffasia* (Ono and Hashim 2008) and even closer to *Asceua*. These have few, very simple conical setae gathered in a shallow, riddled depression, as can also be seen in *Suffasia kanchenjunga* Ono, 2006 (Fig. 4*C*, *D*), *Asceua dispar* (Kulczyński, 1911) (Fig. 4*E*–*G*) and all *Suffrica* species (Henrard and Jocqué 2015, figs 17–20). Our cladistic analysis shows that the SF and DF clades clearly constitute monophyletic entities with a sister-group relationship. However, considering the further morphological differences between the taxa with simple femoral organ setae and those with grooved or barbed setae (Jocqué and Billen 1987; Jocqué 1988), it may be questioned whether the femoral organ has developed twice. This is important because it would perhaps allow the re-establishment of the subfamily 'Storeninae' for those taxa with chisel-shaped setae. The alternative would be the erection of another subfamily for the DF clade, separate from the Zodariinae (SF clade) and the 'Storeninae'. The latter would be characterised by the presence of chisel-shaped setae in combination with the absence of femoral organs. An analysis that focuses on these questions is underway.

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Handling editor: Mark Harvey

Appendix 1. List of taxa (other than *Suffascar*) used in the cladistics analysis with collection information

1. *Hermippus loricatus* Simon, 1893: 1♀, D.R. CONGO, Lubumbashi, Mikembo sanctuary, gallery forest, along the river, 11°28′S 27°39′E, 13.i.2011, hand collecting, 'N15', Jocqué R. and Hasson M. (MRAC 245363; DNA Z073); 2♂, D.R. CONGO, Lubumbashi, Mikembo sanctuary, 'wektree', 8.xi.2010, hand collecting, 'BAK19', Jocqué R. (MRAC 245362).
2. *Mallinella vokrensis* (Bosmans & van Hove, 1986): 1M, CAMEROON, Faro Game reserve, gallery forest, 17.iv.2007, sieving, Jocqué R., Loosveldt K., Baert L. and Alderweireldt M. (MRAC221266; DNA Z148); 1♀, CAMEROON, Faro Game reserve, mature gallery forest, 05.v.2007, pitfall, Jocqué R., Loosveldt K., Baert L. and Alderweireldt M. (MRAC221221; DNA Z148).
3. *Heliconilla* cf. *globularis* Dankittipakul, Jocqué & Singtripop, 2012: 1♂, THAILAND, Surat Thabi Prov. Ko Samiu, Nathon Distr. Hin Lad Waterfall, primary forest near stream, 100 m asl, 9°31′15″N 99°57′47″E, 5–6.vii.2011, Schwendinger P. (MHNG TH-11/05; DNA Z242).
4. *Heradion paradiseum* (Ono, 2004): 1♂, VIETNAM, Evergreen forest SE of Tam Dao city, 1000–1200 m asl, 21°26′49″N 105°39′06″E, 13–14.*v*.2012, Schwendinger P. and Schultz A. (MHNG VN-12/03c; DNA Z241).
5. *Asceua lejeunei* Jocqué, 1991: 1♂, GUINEA, Mont Nimba, 'Gouan Forest' (Mid-one), N 07°42′03″N 08°23′58″W, litter from branches in trees and shrubs at 1,5–3 m above the floor, 08.x.2011, Nim-100, Henrard A. and Van den Spiegel D. (MRAC 245358; DNA Z029); 2♂ 1♀, GUINEA, Mont Nimba, Seringbara Forest, 606 m asl, 13.iii.2012, secondary forest, canopy fogging, Henrard A., Allard C., Bimou P., Sidibe M. and Van den Spiegel D. (MRAC 239640).
6. *Asceua* cf. *dispar* (Kulczyński, 1911): 1♂, MALAYSIA, Singapore, Pulau Semakau, 31.v.2012, SMO3 (The mangrove project), Grootaert P. (RBINS 29265; DNA Z281).
7. *Asceua gruezoi* Barrion & Litsinger, 1992: 1♂ 1juv., PHILLIPINES, Luzon Island, Laguna Prov., Malaboo camp, Mt Makiling, 3.46 km SSW Los Baños, 673 m asl, 14°08.220′N 121°12.352′E, 10–12.v.2011, propylene glycol pitfall traps forest, PH0004, Wood H., Yngente M., Choussou Polydouri N., Griswold C., San Juan V. and Knutson V. (CASENT 9043514; DNA Z296 (male)); 1M 1♀ 1juv., same data as previous (CASENT 9043515; DNA Z296 (juv.)).
8. *Suffrica exotica* Henrard & Jocqué, 2015: 33♂ 17♀, TANZANIA, Mkomazi Game Reserve, Ibaya, Igire Ridge, 1200 m, 3°58′S 37°46′E, 24.xi.1994, litter of dry forest, crest of ridge, Russell-Smith A. (MRAC 241686).
9. *Suffrica gus* Henrard & Jocqué, 2015: 2♂ 2♀ paratype, TANZANIA, Tanga, East Usambara Mts., Amani, 5°5.7′S 38°38′E,950 m, 28.x–9.xi.1995, pitfalls, C. Griswold, N. Scharff and D. Ubick (MRAC 245359).
10. *Suffasia tumegaster* Jocqué, 1992: morphological information taken from the original description.
11. *Suffasia kanchenjunga* Ono, 2006: 1♂ 1♀: NEPAL, Panchthar district, Dhorpar Kharka, mature Rhododendron-Lithocarpus forest, 2700 m asl, 13–16.iv.1988, Martens J. and Schawaller W. (coll. Martens N°324).
12. *Acanthinozodium sericeum* Denis, 1956: MOROCCO: Tiznit, Goiurizim 5 km E., Stones in Argania steppe, 26.iv.2012, hand catch, Bosmans R. (Coll. Bosmans R.; DNA Z132).
13. *Zodarion nitidum* (Audouin, 1826): 1♀, ISRAEL, Negev, Sede Boqer, Ein Avedat, 400–480 m asl, 30°50′54.80′N 34°44′57.08′E, 04.ix.2011, under stones below shrubs, in small caves, Jäger P. (SMF 109; DNA Z268).
14. *Tropizodium siam* Dankittipakul, Jocqué & Singtripop, 2012: 1♂, THAILAND, I–ii.2013, Vanuytven H.
15. *Palaestina expolita* O. Pickard-Cambridge, 1872: 1♂, GREECE, Cyclades, Thira, Santorini, Kamari, 38 m asl, 36°22′53.76″N 25°28′30.18″E, 31.vii.2010, open habitat, Rec. Nissen K. (Coll. Lissner J., Reference ID 6836; DNA Z319).
16. *Trygetus sexoculatus* (O. Pickard-Cambridge, 1872): 1♂ 1♀, Egypt, Sinai, 50 km E of Suez, 31.iii.2000, Alderweireldt M. (MRAC 209667; DNA Z234 (female)).
17. *Akyttara homunculus* Jocqué, 1991: 1♂, D.R. CONGO, Lubumbashi, Mikembo sanctuary, miombo woodland (Uapaca trees), 11°28′S 27°39′E, 26.xi.2010, pitfall traps, Jocqué R. (MRAC 234411; DNA Z108): 2♂ 3♀, further data as previous, 3–15.xi.2010, fogging (MRAC 242493).
18. *Heradida speculigera* Jocqué, 1987: 1♂, SOUTH AFRICA, Western Cape province, Sawadee, 344 m asl, 01.iii.2007, pitfall trap, E. Nortje and S. Kritzinger-Klopper, (number 3.3.7; DNA Z009); 1♀ holotype, SOUTH AFRICA, Western Cape province, Clanwilliam, Cederberg, 500–1000 m asl, viiI–1962, in humus under bushes or stones, Leleup N. (MRAC 132618); 2♂ 2♀, SOUTH AFRICA, Cederberg, Sanddrif, 11.iii.1993, Rocky area, in leaf litter at foot of rocky outcrop, Jocqué R. (MRAC 174705).
19. *Diores poweri* Tucker, 1920: 1♀, SOUTH AFRICA, Free State Province, Bloemfontein, National Botanic Gardens, 29°02′S 26°12′E, 28.xi.2012, pitfalls in grassland, Haddad C. (DNA Z312).

CHAPTER IV

ZODARIIDAE PHYLOGENY: A COMBINED ANALYSIS

The discovery of paired femoral glands in the new taxa *Suffrica* Henrard & Jocqué, 2015, *Suffascar* Henrard & Jocqué, 2017 and some other representatives of the Zodariinae was followed by a cladistic analysis (Henrard and Jocqué 2017). Based on morphology and mainly focusing on groups of taxa characterized by femoral organs, the analysis showed that the "single femoral organ" (SF) and the "dual femoral organ" (DF) clades constitute two separate entities. The two clades clearly share a sister-group relationship although only the monophyly SF clade was strongly supported. This preliminary analysis also hinted at the possibility that the Storeninae (paraphyletic in Jocqué 1991a) should be re-established. During the examination of material used for DNA analyses and morphological character scoring, some taxa characterized by remarkable combinations of features appeared new to science and were described (Henrard and Jocqué 2015; Jocqué and Henrard 2015a; 2015b; 2015c; 2018; Haddad, Henrard and Jocqué 2019). Those recently described taxa were from tropical Africa, where the Zodariidae diversity is remarkably high. Numerous other unknown zodariid taxa remain to be described from Africa but also from other tropical continents. However, the character set and the number of taxa used in this study was fairly complete and doubtlessly sufficient for the analyses on a global scale and to test different hypotheses, including the re-establishment of the Storeninae.

Paper in preparation

Henrard, A. & Jocqué, R. (in prep.). Phylogeny of the ant-eating spiders (Araneae; Zodariidae): a combined analysis.

PHYLOGENY OF THE ANT-EATING SPIDERS (ARANEAE; ZODARIIDAE): A COMBINED ANALYSIS

Henrard A. & Jocqué R.

ABSTRACT

The phylogeny of the family Zodariidae Thorell, 1881 is revised on a global scale using morphological and molecular data. The present study represents the largest taxonomic sample of Zodariidae analyzed to date. A character matrix was built, comprising in 153 characters spread over 11 morphological groups. The molecular data included 5 genetic markers: 1 mitochondrial (COI) and 4 nuclear markers, including sequences of protein coding genes (Act5C, H3) and ribosomal genes (18S, 28S). In order to assess the phylogeny of the Zodariidae, different analyses were performed (based on morphological, genetic and combined datasets) using different statistical approaches (Maximum Likelihood, Bayesian inferences and parsimony for morphological data). The combined results highlighted 5 groups corresponding to 5 sub-families. As predicted, Cyriocteinae appeared sister to all remaining Zodariidae in the morphological analysis. However, this finding could not be confirmed by the molecular analysis due to the lack of fresh biological material. The Lachesaninae, Cryptothelinae and the Zodariinae were redefined. The Storenomorphinae were found paraphyletic in the molecular and combined analyses and fell into the Cryptothelinae. As a consequence, Storenomorphinae were fused into the Cryptothelinae. The Storeninae were re-established and redefined. *Procydrela procursor* Jocqué, 1999 could not be assigned to any subfamily and it may be considered to put it in a group of its own. Among the Zodariinae, the femoral organ clades (DF+SF) were strongly supported in the combined analysis. Surprisingly the molecular analyses only supported the SF clade. However, even based on the morphological and combined analysis, the evolution of the femoral organ and its complexity remain ambiguous and not fully resolved.

KEYWORDS

Systematics, cladistics, multigene analysis, morphology, burrowing spiders

INTRODUCTION

Size and Range

The Zodariidae Thorell, 1881 (Figs 4-3), commonly named "burrowing spiders" or "ant-eating spiders", represent a medium sized family of spiders. With 1143 zodariid species disseminated in 85 genera, they rank 12th of the most diverse spiders families according to the World Spider Catalog (WSC) (2018). Zodariids are mainly distributed in tropical and subtropical regions whereas few genera have reached the temperate region (Jocqué and Dippenaar-Schoeman 2007). Some taxa display a typical distribution pattern, with representatives restricted to the southern parts of some continents only. This is the case for *Australutica* Jocqué, 1995 restricted to southern Africa and southern Australia and *Cyrioctea* Simon, 1889 also found in South America. Such distributions are assumed to be an echo of Gondwanaland and subsequent continental drift after its break up (Jocqué 1993; 2008; 2013; Murphy and Roberts 2015). Other zodariid taxa, such as *Mallinella* Strand, 1906 or *Asceua* Thorell, 1887, seem instead to have reached some part of the world mainly by dispersion (Jocqué 1993; Dankittipakul et al. 2012). The highest diversity of zodariid genera occurs in Africa (44%) and Australia (37%), followed by Far East (23%), Palearctic (13%) and South America (11%) (WSC 2018). North America harbors only two genera: *Lutica* Marx, 1891, (Fig. 1D) endemic to the southern coast and offshore islands of California (Ramírez 1995) and *Zodarion* Walckenaer, 1826, represented by some introduced species in Canada and the USA (Vogel 1968; Bosmans 1994; Paquin and Dupérré 2006).

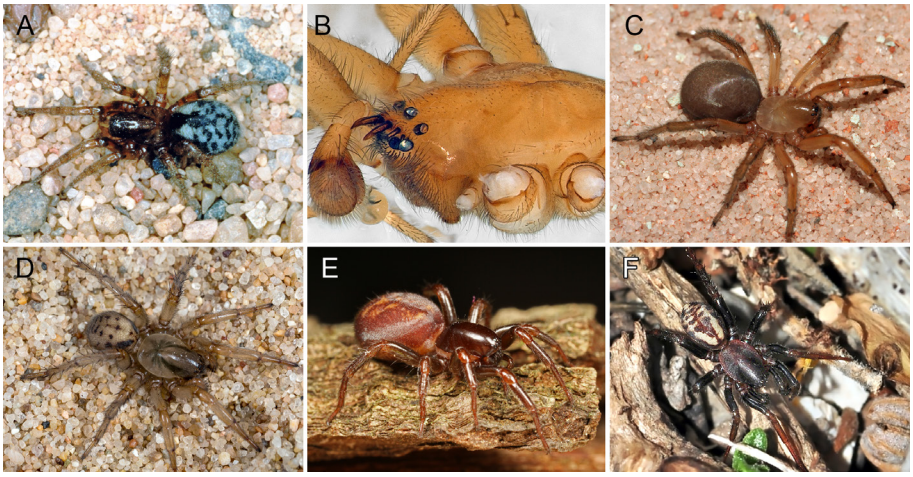


Figure 1. Habitus of some Cyriocteinae and Lachesaninae species. A. *Cyrioctea* sp. Simon, 1889, female, Chile, © James Cokendolpher. B. *Cyrioctea marken* Platnick & Jocqué, 1992, male, detail of carapace (photo in alcohol) Limpopo, South Africa © Arnaud Henrard. C. *Lachesana blackwalli* (O. Pickard-Cambridge, 1872), sub-adult female, Negev, Israel © Rudolf Macek. D. *Lutica* sp. Marx, 1891, female, California, USA © Alice Abela. E. *Selamia reticulata* (Simon, 1870), female (specimen DNA Z075), Aude, France © Arnaud Henrard. F. *Amphiledorus* sp. Jocqué & Bosmans, 2001, male, Valencia, Spain © Francisco Rodriguez Luque.

Natural History

The zodariids are wandering, mainly nocturnal ground-dwelling spiders. They apparently have never been observed to perform ballooning (Ramírez 1995; Pekár 2002), a dispersal behavior used by numerous spider taxa (Bell et al. 2005). They are well represented in the ground-dwelling spider assemblage (e.g. Russel Smith et al. 1987; Jocqué 1991a; Russell-Smith 1999; 2002; Haddad et al. 2013; Jansen et al. 2013; Russell-Smith and Jocqué 2015) even if species diversity (and abundance) is often relatively modest compared to that of other ground-active spider families (e.g. Salticidae, Lycosidae). However, forest-dwelling zodariids are among the families with the greatest number of species and specimens collected in pitfall traps. Many species occur in arid or semiarid areas, living in the sand, among rocks or in vegetation.

Figure 2. Habitus of some Cryptothelinae species. A. *Storenomorpha* sp. Simon, 1884, Cuc Phuong National Park, Vietnam © Marcus Ng. B. *Chariobas lineatus* Simon, 1893, female, Eastern Cape, South Africa © De Moor Ferdie. C. *Thaumastochilus* sp. Simon, 1897, Tete province, Mozambique © Jo DA Nobrega. D. *Cicynethus* cf. *decoratus* Simon, 1910, male, KwaZulu-Natal, South Africa © Suncana Bradley. E. *Cryptothele* cf. *doreyana* Simon, 1890, Queensland, Australia © Cameron de Jong. F. *Cydrela schoemanae* Jocqué, 1991, male, Gauteng, South Africa © Peter Webb. G. *Psammoduon canosum* (Simon, 1910), Northern Cape, South Africa © Neville Cornberg. H. *Systenoplacis vandami* (Hewitt, 1916), Gauteng, South Africa © Peter Webb. I. *Psammorygma* sp. Jocqué, 1991, KwaZulu-Natal, South Africa © Warren Schmidt.

Some genera appear to be strongly tied to rainforest, living mainly in the leaf litter (e.g. *Mallinella* Strand, 1906 (Figs 4B, C), *Dusmadiores* Jocqué, 1987) but also in vegetation, on bushes or trees (e.g. *Asceua* Thorell, 1887 (Fig. 4D); *Storenomorpha* Simon, 1884 (Fig. 2A)). Most of the ground-dwelling spiders have conspicuous adaptations for burrowing, such as numerous strong spines on the palps and the posterior legs, as well as a high carapace accommodating strong muscles for digging.

Figure 3. Habitus of some Storeninae species. A. *Cybaeodamus taim* Lise, Ott & Rodrigues, 2009, female, Mendoza, Argentina © Cristian Grismado. B. *Leprolochus birabeni* Mello-Leitão, 1942, Río Negro, Argentina © Julián Tocce. C. *Platnickia bergi* (Simon, 1895), female with its eggs sac, Tierra del Fuego, Argentina © Cristian Grismado. D. *Australutica manifesta* Jocqué, 1995, male, Western Australia © Robert Whyte. E. *Storosa obscura* Jocqué, 1991, male, South Australia © Allan Lance. F. *Storena colossea* Rainbow, 1920, male, Queensland, Australia © Robert Whyte. G. *Neostorena* sp. Rainbow, 1914, male, South Australia © Allan Lance. H. *Euasteron enterprise* Baehr, 2003, female, Queensland, Australia © Robert Whyte. I. *Subasteron daviesae* Baehr & Jocqué, 2001, female, Queensland, Australia © Greg Anderson. J. *Habronestes bradleyi* (O. Pickard-Cambridge, 1869), male, South Australia © Greg Anderson. K. *Habronestes* sp. L. Koch, 1872, female with ant as prey, South Australia © Mark Newton. L. *Zillimata scintillans* (O. Pickard-Cambridge, 1869), female, Western Australia © Farhan Bokhari. M. *Masasteron* sp. Baehr, 2004 or *Holasteron* sp. Baehr, 2004, male, South Australia © Allan Lance.

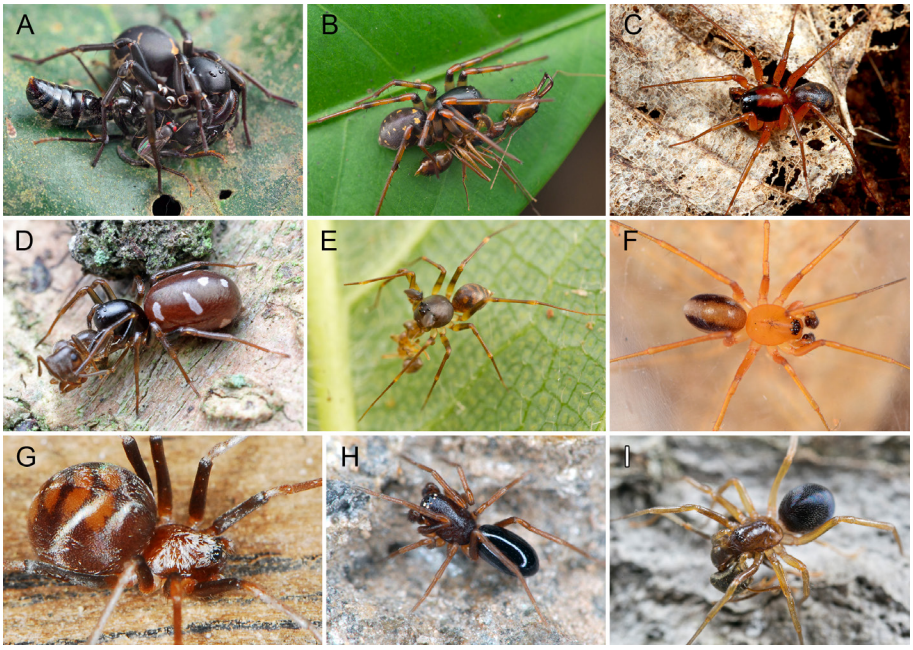


Figure 4. Habitus of some Zodariinae species. A. *Hermippus* cf. *arcus* Jocqué, 1989, male, Udzungwa, Tanzania © Paul Bertner. B. *Mallinella* sp. Strand, 1906, female with ant as prey, North Region, Singapore © Nicky Bay. C. *Mallinella* sp. Strand, 1906, male, Nimba, Guinea © Arnaud Henrard. D. *Asceua japonica* (Bösenberg & Strand, 1906), female with ant as prey, Fukuoka, Japan © Takashi Komatsu. E. cf. *Suffasia* sp. Jocqué, 1991, male with ant as prey, Central Region, Singapore © Nicky Bay. F. *Diores* sp. Simon, 1893, male, Western Cape, South Africa © Peter Webb. G. *Ranops* sp. Jocqué, 1991, female, Mpumalanga, South Africa © Peter Webb. H. *Palaestina expolita* O. Pickard-Cambridge, 1872, male, Cyclades, Greece © Jørgen Lissner. I. *Zodarion nigrifemur* Caporiacco, 1948, female with ant as prey, Antalya, Turkey © Arnaud Henrard.

Psammoduon Jocqué, 1991 (Fig. 2G) has a remarkable habit of flipping over its back when burrowing and stays upside down just under the sand surface to catch wandering prey, hence their nickname of "back-flip spiders" (Newlands and De Meillon 1986; Jocqué 1991b). Another remarkable feature are the transverse rows of sturdy spines among the eye rows in some genera (i.e. *Cyrioctea* (Figs 1A, B) and *Leprolochus* Simon, 1893 (Fig. 3B)), which are assumed to constitute a burrowing device (Platnick 1986; Platnick and Griffin 1988; Jocqué 1988a; 1991a; 2013). These spiders live under ground

and rarely come to the surface. The females, which hardly ever emerge from their burrows, are rarely collected. Some species, often robustly built burrowers, not only live in the sand or underground, but also build a silk-lined burrow provided with a trapdoor as retreat (e.g. *Antillorena* Jocqué, 1991, *Capheris* Simon, 1893, *Psammorygma* Jocqué, 1991 (Fig. 2I), *Neostorena* Rainbow, 1914 (Fig. 3G)) (Gertsch 1961; Jocqué 1991a;). Exceptions to the ground-living behavior occur in genera adapted to a life in vegetation. Some spiders such as *Chariobas* Simon, 1897 (Fig. 2B), *Thaumastochilus* Simon, 1893 (Fig. 2C) or *Cicynethus* Simon, 1910 (Fig. 2D) that live among shrubs or trees have a peculiar elongate morphology, which is nicely well adapted for fitting tubular retreats (Leroy and Jocqué 1993; Jocqué and Henrard 2018; new obs., see Appendix 1). The zodariids that have the ability to burrow are often named "burrowing spiders".

There are zodariids that, however, do not burrow but construct retreats with soil particles or plant debris. Those retreats can be hemispherical, "igloo-shaped" (e.g. *Zodarion*, *Habronestes* L. Koch, 1872) or completely spherical (e.g. *Mallinella*, pers. obs.) and are most often located under stones or hidden in the litter. This behavior is probably derived from a simple digging habit combined with the construction of an underground silk-lined retreat (Jocqué 1991a). This group of spider is often called "ant-eating spiders" as they are essentially, if not compulsory ant or termite eaters (Jocqué 1988b; Jocqué and Dippenaar-Schoeman 1992; Pekár 2004, Pekár et al. 2005; Cárdenas et al. 2014; Komatsu 2016).

Some taxa belonging to the ant-eating group are characterized by the presence of a gland on the femur of the legs, called "femoral organ", which is supposed to be linked to their strongly specialized diet (Jocqué and Billon 1987; Jocqué 1988b; Pekár and Šobotník 2007; Henrard and Jocqué 2015). Although the structure of the gland is known to have an exocrine function (Pekár and Šobotník 2007), the compound of the secretion and its exact role remain mysterious.

This organ was first assumed to be unique on the femur (Jocqué and Billen 1987; Jocqué 1988b; Pekár and Šobotník 2007). However, recent studies have shown that some taxa have a pair of femoral organs on each leg (enrard and Jocqué 2015; Henrard and Jocqué 2017a). Zodariid spiders characterized by the presence of a femoral organ on the legs are known to feed exclusively on ants. They even reject any other preys that have been offered in laboratory experiments (Pekár and Toft 2009). Some taxa, such as *Zodarion* or *Trygetus* Simon, 1882 species, have an even narrower trophic niche, consuming only their model ants (Pekár and Král 2002; Pekár et al. 2005; 2012a). As compared to burrowing spiders, ant-specialized zodariids have slender legs, allowing them to run fast and avoid counter-attacks by ants (Pekár et al. 2013). The legs are also provided with a crack (located in the patellae) that enables autospasy, facilitating the escape from ants if bitten (Jocqué and Dippenaar-Schoeman 1992).

The venom of these specialized ant-eating spiders is often specific and efficient only to a restricted range of prey, even at specific level (Pekár et al. 2008; 2014; 2018b; Pekár 2009; Pekár et al. 2018b). Their chelicerae are fused and not so robust, bearing very short fangs that allow penetration, in a particular way, of the softer cuticle of ant legs (Pekár and Král 2002; Pekár 2004). The preying behavior of the short-fanged species is characterized by a short attack during which the ant is stabbed and injected with venom. Typically, the spider then retreats and waits until the ant succumbs to start feeding. On the other hand, the most plesiomorphic representatives of the burrowing spiders are instead more generalist predators and may also eat other invertebrates (Simon 1910; Ramírez 1995; Rössl and Henschel 1999; Pekár et al. 2013; Pekár and Toft 2009; 2015). They have stronger legs that allow them to grab and hold the prey firmly during the attack (Pekár and Lubin 2009; Pekár et al. 2013). Representatives of plesiomorphic burrowing genera also have stronger and free chelicerae with larger fangs than those of specialized ant-eaters, being probably more powerful to penetrate the thick cuticle of larger prey.

In addition to that, the complexity of venom components of non-specialized taxa is also more varied, allowing a wider trophic niche (Pekár et al. 2018a). It was shown that the predatory behavior can be different if the prey is potentially dangerous (like ants) or relatively harmless (Pekár and Lubin 2009; Pekár et al. 2013). In Zodariidae, myrmecophagy is viewed as a derived trophic strategy (Pekár et al. 2012a; Pekár et al. 2013; Pekár and Toft 2015).

Systematics and phylogeny

The Zodariidae are among the most diversified spider families, having an impressive size range and an enormous variation of shapes (Jocqué 1991a; Jocqué et al. 2013; Jocqué and Dippenaar-Schoeman 2007; Russell-Smith and Jocqué 2015). The family was already fairly well defined by Simon (1870). In the revision at generic level by Jocqué (1991a), the definition was corroborated in a phylogeny, although the status of some taxa remained questionable (e.g. *Cryptothele*, *Cyrioctea*). The Zodariidae were then characterized by a combination of morphological characters including the absence of a serrula on the endites, the stronger anterior lateral spinnerets (ALS) (compared to the others) and the laterally inserted teeth on the tarsal claws (Jocqué 1991a; Jocqué and Dippenaar-Schoeman 2007). However, these characters, taken independently, are also present in various taxa belonging to other families (Ramírez et al. 2014).

A recently discovered synapomorphy, a rounded, sclerotized prolateral projection on the distal rim of all leg tibiae, fitting in a metatarsal pouch (Jocqué and Henrard 2015b), strongly consolidated the diagnosis of the family and removed any doubt on the inclusion of plesiomorphic taxa and *Cryptothele*. However, until recently, the phylogenetic placement of the Zodariidae itself was not totally clear (e.g. Coddington and Levi 1991; Coddington et al. 2004; Coddington 2005; Dippenaar-Schoeman and Jocqué 1997; Jocqué and Dippenaar-Schoeman 2007).

The family was sometimes associated with Homalonychidae (Simon 1893; Roth 1984; Wunderlich 2004), or considered part of the Amaurobioidea (Jocqué and Dippenaar-Schoeman 2007), or placed in a polytomy with Dionycha and Amaurobioidea (Coddington and Levi 1991; Coddington et al. 2004; Coddington 2005; Ramírez 2014).

Miller et al. (2010a) were the first to incorporate representatives of the Zodariidae in a comprehensive molecular phylogenetic analysis. The family was part of the RTA clade and showed a strong sister-group relationship with the peculiar cribellate Penestomidae. This placement was recently corroborated by Dimitrov et al. (2017), who used the same sequences in their analyses and by Wheeler et al. (2017), who used a higher number of representatives and confirmed as well the monophyly of the Zodariidae with *Cyrioctea* sister to all remaining zodariids groups, as predicted by the morphology (Platnick 1986; Platnick and Griffin 1988, Jocqué 1991a).

Until recently, the family placement of *Cryptothele* L. Koch, 1872 remained uncertain for a long time (Jocqué 1991a; Jocqué and Dippenaar-Schoeman 2007; Marusik and Omelko 2013). Originally the genus was placed in its own separate family Cryptothelidae L. Koch, 1872 but later, Simon (1890) placed it as a subfamily in the Zodariidae. Then, the assignment of *Cryptothele* to Cryptothelidae (*e.g.* Davies 1985; Coddington and Levi 1991; Coddington et al. 2004; Coddington 2005; Saaristo 2010; Marusik and Omelko 2012) or Zodariidae (*e.g.* Benoit 1978; Wunderlich 2004; Ramírez 2014) changed several times. The inclusion of *Cryptothele* into a subfamily of the Zodariidae is now very well supported as it was eventually confirmed both by morphological characters (Ramírez et al. 2014; Jocqué and Henrard 2015b) and molecular analyses (Wheeler et al., 2016; *present study*). The separation of Cryptothelidae L. Koch, 1872 as recently proposed by Murphy and Roberts (2015) was thus rejected and although the earlier name “Cryptothelidae” had formal priority,

the family name Zodariidae is amply protected by usage to keep nomenclatorial stability (WSC 2018).

The Homalonychidae also turned out to be a close relative of the Zodariidae and the Penestomidae, although its placement was less stable in the phylogenetic analyses of Miller et al. (2010a) or Wheeler et al. (2017). However, at least one morphological trait characterizes these three families and provides some support to the molecular studies, *i.e.* the major ampullate gland spigots are positioned in the center of the ALS and surrounded by piriform gland spigots (see Ramírez et al., 2014). Even though the placement of the Homalonychidae remains uncertain, they are considered a part of the Zodarioidea (Garrison et al. 2016; Wheeler et al. 2017), a superfamily branching of sister to the highly diverse RTA clade (Wheeler et al. 2017; see also the composite tree of Labarque et al. 2017; fig. 16).

PURPOSES

The cladistic approach used in the study of Jocqué (1991a) was fairly rudimentary and contains some flaws (see Dankittipakul et al. 2012) reflecting the methodology in the early days of cladistics. In his analysis, the outgroup was *Cyrioctea*, which should have been part of the ingroup. Characters thought to be of importance received arbitrarily higher weight. Characters relative to the femoral organ were coded as additive: the evolution of its states was then "forced" and thus not tested. No measures of robustness were calculated for the different clades …

Since the generic revision of Jocqué (1991a), the described diversity of Zodariidae has increased and 37 genera have been added (WSC 2018). To date, mainly internal phylogenetic inferences were focused on some taxa or groups of taxa (*e.g.* Henrard and Jocqué 2017a; see also Dankittipakul et al. 2012 for an exhaustive list) and all have been restricted to morphological characters.

Only few recent studies have tested the main hypotheses focusing on the relationships within the family (Ramírez *et al* 2014; Wheeler et al. 2017). It is remarkable that these recent studies did not fundamentally change the structure of the family as found by Jocqué (1991a). The present study represents the largest taxonomic sample of Zodariidae analyzed to date and firstly aims to infer the phylogeny of the entire family on a global scale using a combined approach of both molecular and morphological data. A related objective of this latter goal is to further investigate the proposed monophyly of the different subfamilies established by Jocqué (1991a; 1992) and test or confirms the placement of some taxa such as *Cyrioctea*, *Cryptothele* and other "problematic" taxa in the Zodariidae. The study of the relationships among its genera will provide the opportunity to understand and interpret the evolution of morphological and behavioral traits, such as the predation on ants, the evolution of the femoral gland, the miniaturization of the species and the direction of complexity changes in the genitalia, a crucial theme in the theory of sexual selection (see Eberhard and Huber 2010; Azevedo et al. 2018).

MATERIAL AND METHODS

Institutions and Museum repositories

CAS	California Academy of Sciences, San Francisco (USA)
CHNUFPI	Universidade Federal do Piauí, Floriano (Brazil)
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge (England)
NCA	National Collection of Arachnids, Pretoria (South Africa)
NHRS	Naturhistoriska Riksmuseet, Stockholm (Sweden)
RBINS	Royal Belgian Institute of Natural Sciences, Brussels (Belgium)
RMCA	Royal Museum for Central Africa, Tervuren (Belgium)
QM	Queensland Museum, Brisbane (Australia)
UCL	Université catholique de Louvain, Louvain-la-Neuve (Belgium)
ZMUC	Zoological Museum, University of Copenhagen (Denmark)

Abbreviations

AER	anterior eye row
BI	bayesian inference
CAH	collection Arnaud Henrard
char., chars	character, characters
DF	dual femoral organ clade
LAS	Leica Application Suite
ML	maximum likelihood analysis
MB	bayesian analysis performed with MrBayes software
PB	bayesian analysis performed with PhyloBayes software
PER	posterior eye row
PLS	posterior lateral spinnerets
PMS	posterior median spinnerets
RTA	retrolateral tibial apophysis
SEM	scanning electron microscope
SF	single femoral organ clade
TNT	Tree analysis using New Technology
WSC	World Spider Catalog

Specimen used for examination and illustrations

Examination and photographs of the habitus, details of mouthparts, legs, detached male palps and female genitalia were done with a Leica MZ16 using the LAS automontage software (ver. 3.8). For SEM photos, dissected body parts and genitals were first immersed in a few ml of acetone 'overnight', then dried by a rapid evaporation of the acetone with a heated plate (set at +- 60°C). Some samples were also used for SEM after having used in the DNA extraction protocol (see Henrard and Jocqué, 2015, Henrard and Jocqué 2017a). The dried body pieces were then gold coated and examined or photographed with a JEOL 6480 LV scanning electron microscope. Illustrations were assembled and edited in Photoshop CS5 (white balance and level adjusted).

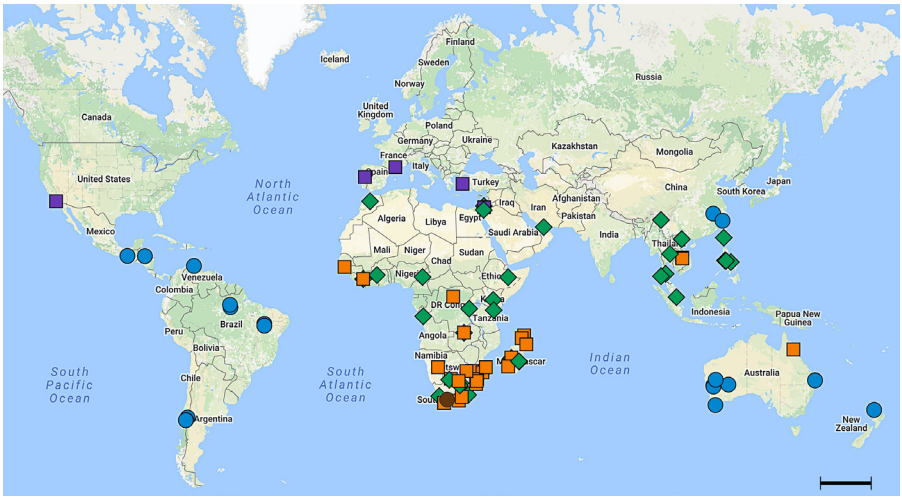


Figure 5. Distribution map of all zodariid samples included in our molecular study (created with Google My Maps and edited in Photoshop CS5). Purple squares represent Lachesaninae representatives, brown circle *Procydrela*, orange squares Cryptothelinae, green lozenges Zodariinae and blue circles Storeninae. Scale = 2000 km.

Taxon sampling

The taxa studied in this work were obtained from different sources (institutions or collectors) stemming from different places over the world (Fig. 5; see also Appendices 1 to 3 for detailed lists). Some specimens sequenced during this study were freshly collected by the authors (mainly between 2011-2013) using various sampling methods (e.g. hand collecting, beating, fogging, sieving, using thermal vacuum, pitfall trapping with propylene glycol, etc.) and then usually preserved in 95% alcohol, otherwise in 70% alcohol. For other material that was sent to us or was obtained from collections, dating back from 1999 to 2014, fixation and preservation conditions may have varied. For five taxa, we used extracted total DNA samples that have been used in the study of Miller et al. (2010a). *Penestomus egazini* Miller, Griswold & Haddad, 2010, *P. prendinii* Miller, Griswold & Haddad, 2010, *cf. Aschema sp*., *Chumma inquieta* Jocqué, 2001 and "*Zodarion sp*." (actually *Diores* sp.) were kindly provided by Jeremy Miller and labeled here Z282 to Z286 respectively.

The molecular analyses include in total 120 sequenced taxa (113 Zodariidae and 7 non-Zodariidae) plus additional 6 taxa for which sequences were available on GenBank, representing Zodariidae, Agelenidae, Amaurobiidae, Ammoxenidae, Chummidae, Corinnidae, Ctenidae, Penestomidae. A few extra taxa representing Titanoecidae were included as outgroup taxa as they may be sister to all remaining taxa used in this study (see Ramírez 2014; Labarque et al. 2017; Henrard and Jocqué 2017b; Wheeler et al. 2017). They are actually part of the so-called, highly diverse, RTA clade. Among the Zodariidae, 59 known genera could be sequenced, representing roughly 70% of all known genera in the family. Appendices 1 to 3 list all the specimens used in this study (for molecular and/or morphological purposes) with detailed collection information. Unfortunately we could not obtain any molecular data from any *Cyrioctea* tested in this study, *i.e. Cyrioctea griswoldorum* Platnick & Jocqué, 1992 (RMCA_ARA_217636; DNA Z215), *C. marken* Platnick & Jocqué, 1992 (RMCA_ARA_245374; DNA Z321) and *C. sawadee* Jocqué, 2013 (NCA; DNA Z299).

Morphological analysis

Character sampling

The morphological analyses were partly based on those of Jocqué (1991a), Ramírez et al. (2014) and Henrard and Jocqué, 2017). The data matrix was updated by addition/deletion of characters and states for some characters. Since Jocqué (1991a), almost 40 genera were added to the family, now comprising 84 genera. Most of them could be included in the morphological analysis excepted the four following genera: *Leviola* Miller, 1970, *Malayozodarion* Ono & Hashim, 2008 *Nosterella* Baehr & Jocqué, 2017 and *Zodariellum* Andreeva & Tyschchenko, 1968. Representatives of some genera were not directly examined with a stereomicroscope and, in those cases, sufficient data were obtained from in the literature.

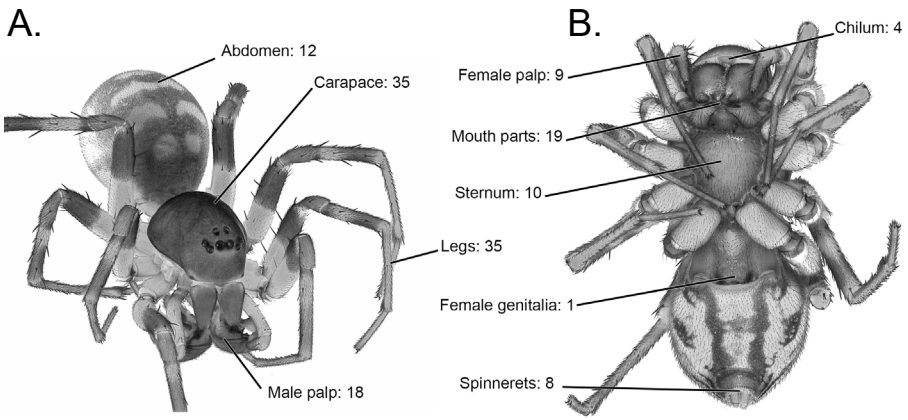


Figure 6. Distribution of characters used in the morphological analysis depicted on an undescribed Afrotropical *Mallinella* species ('spAH002'). A. Male, frontal, slightly oblique view. B. Female, ventral view.

The relationships among the outgroup taxa were not the primary focus of the present study, and therefore the outgroup taxon sample is clearly less exhaustive than for the ingroup. However, we did chose some representatives of other families (Agelenidae, Amaurobiidae, Penestomidae, Titanoecidae) that could represent a putative sister group.

The character matrix (Appendix 4) comprises 131 taxa and 153 characters spread over 11 morphological groups (see Fig. 6) of which 35 are from the carapace, 4 from the chilum, 10 from the sternum, 19 from the mouth parts, 35 from the legs, 18 from the male palp, 9 from the female palp, 1 from the female genitalia, 12 from the abdomen, 8 from the spinnerets, and two extra characters relative to the cribellum and calamistrum (characters and their states are listed and illustrated in Appendix 5). Non-applicable or unknown states are presented as '?'. Excel was firstly used to build the character matrix then Mesquite (version 3.04) was used to edit and to export the matrix into the format needed for the analyses in TNT and WINCLADA.

Phylogenetic analyses – morphological data

The parsimony analysis was carried out using the traditional search in TNT 1.1 (Goloboff, Farris and Nixon 2008) run through NONA 2.0 (Goloboff 1993). All multistate characters were coded as non-additive. The most parsimonious trees were found using the tree bisection and reconnection (TBR) swapping algorithm (with 1000 replications and 10 trees to save per replication) and with all characters equally weighted (tree in Appendix 6). In order to study different possible topologies, the dataset was also analyzed *a posteriori* under regimes weighting against homoplasy (Goloboff 1993). Implied weighting was used with different values of the constant of concavity (K=2 to 10) and using the same parameters as described above (see Appendix 7 for detailed tree with K=4). The majority rule consensus tree was then estimated with a cut off value of 50. The resulting trees were then imported in WINCLADA 1.00.08 (Nixon 1999–2002), which was used to show the character changes.

As measures of branch supports we calculated bootstraps, Bremer support and posterior probabilities. Bootstraps (1000 replications and output results as absolute frequencies) and Bremer (absolute) support were obtained with TNT 1.1 (also using TBR). For Bremer calculation, analyses searching suboptimal trees were performed for trees suboptimal by 0.2, 0.5, 1, 2, 3, 4 and 5 steps. Posterior probabilities were estimated with MrBayes with the format data type treated as "standard" and the following settings: nst=1, rates=gamma, coding=variable. MB analyses were conducted for 10,000,000 and it was checked that the standard deviation of split frequencies have been decreased below 0.01. The tree search was conducted according to MrBayes defaults (two independent runs each consisting of one cold and three heated MCMC chains) (Bayesian morphology-based tree available in Appendix 8).

Table 1. Information on the primers (names, strand direction - forward (F) or reverse (R) - sequences and sources) used in this study for the amplification and sequencing of the studied markers.

Marker	Primer name	F/R	Primer sequence	Reference
COI	C1-J-1718-spider	F	5'-GGNGGATTTGGAAATTGRTTRGTTCC-3'	Vink *et al.* 2005
	C1-N-2568	R	5'-GCTACAACATAATAAGTATCATG-3'	Hedin and Maddison 2001
	C1-J-1517	F	5'-AATCATARGGATATTGGAAC-3'	Thomas and Hedin 2008
	LCO1-1490	F	5'-GGTCAACAAATCATAAAGATATTG-3'	Folmer *et al.* 1994
	C1-N-2776-spider	R	5'-GGATAATCAGAATANCGNCGAGG-3'	Vink *et al.* 2005
H3	H3aF	F	5'-ATGGCTCGTACCAAGCAGACVGC-3'	Colgan *et al.* 1998
	H3aR	R	5'-ATATCCTTRGGCATRATRGTGAC-3'	Colgan *et al.* 1998
	H3F1	F	5'-GTAAAAGTACCGGVGGHAARGC-3'	Colgan *et al.* 1998
Act5C	Actin5C-F-229	F	5'-AAGTATCCNATTGAGCATGGTATTG-3'	Vink *et al.* 2008
	Actin5C-R-1057	R	5'-TTNGADATCCACATTTGTTGGAA-3'	Vink *et al.* 2008
	ActMBF2	F	5'-GCTCCYTTRAATCCHAAAG-3'	Bodner and Maddison 2012
18S	1F	F	5'-TACCTGGTTGATCCTGCCAGTAG-3'	Richter *et al.* 2007
	5R	R	5'-CTTGGCAAATGCTTTCGC-3'	Richter *et al.* 2007
	3F	F	5'-GTTCGATTCCGGAGAGGGA-3'	Richter *et al.* 2007
	Bi	R	5'-GAGTCTCGTTCGTTATCGGA-3'	Richter *et al.* 2007
	A2.0	F	5'-ATGGTTGCAAAGCTGAAAC-3'	Richter *et al.* 2007
	9R	R	5'-GATCCTTCCGCAGGTTCACCTAC-3'	Richter *et al.* 2007
28S	28S-A	F	5'-GACCCGTCTTGAAACACGGA-3'	Giribet *et al.* 1999
	28S-Bout	R	5'-CCCACAGCGCCAGTTCTGCTTACC-3'	Giribet *et al.* 1999
	28s-rD4.8a	F	5'-ACCTATTCTCAAACTTTAAATGG-3'	Schwendinger and Giribet 2005
	28s-rD7b1	R	5'-GACTTCCCTTACCTACAT-3'	Schwendinger and Giribet 2006

Table 2. New internal primers developed in this study (with names, strand direction – forward (F) or reverse (R) – and sequence details) for the amplification and sequencing of the targeted genes.

Marker	New Primer	F/R	Sequence	Reference
H3	H3-ZF	F	5'-AGTACYGGRGGYAARGCCCC-3'	This study
	H3-ZR	R	5'-GCGCACARRTTKGTATCYTCGAAC-3'	This study
18S	18S-Z1bF	F	5'-AGGCGAAACCGCGAATGGCTCA`-3'	This study
	18S-Z2F	F	5'-GCGGTTAAAAAGCTCGTAGTTGC-3'	This study
	18S-Z3aR	R	5'-GCACTCTAATTTTTTCAAAGTAAA-3'	This study
	18S-Z3cR	R	5'-CAACAAAATAGAACCKAGGTCC-3'	This study
	18S-Z3eR	R	5'-CGGATCGCTGGCTGGCATCGTT-3'	This study
	18S-Z4R	R	5'-CAAGAAAGAGCTCTYAATCTGTC-3'	This study
	18S-Z5R	R	5'-AACCTTGTTACGACTTTYRCTT-3'	This study
	18S-A2.0-ZF1	F	5'-GTATGGTTGCAAARCTKAAAC-3'	This study
	18S-A2.0-ZF2	F	5'-CCGGGGGAAGTATGGTTGCA-3'	This study
28S	28S-Z1F	F	5'-GGAGTCYARCATGTRCGCGAGTC-3'	This study
	28S-Z2bF	F	5'-CGGTAAAGCGAATGATTAGAGGC-3'	This study
	28S-Z3R	R	5'-AGTTGCTTCGGCMGGTGAGTT-3'	This study
	28S-Z3bR	R	5'-AGCGCCATCCATTTTCAGGGC-3'	This study
	28S-Z3cR	R	5'-CGGCCGGGTATGGGCTCGACGCTG-3'	This study
	28S-Z4bR	R	5'-GGCACGAAAATCACACYMTCTC-3'	This study
	28S-Mal-A	F	5'-CCAAGGAGTKGAACATGTGCGCG-3'	This study
	28S-Mal-Bout	R	5'-CCCRCAGCGCCAGTTCTGCTTACC-3'	This study

Molecular analysis

Genetic marker choice

Genes were chosen on the base of a literature study (*e.g.* Hormiga, Arnedo and Gillespie 2003; Hedin and Bond 2006; Maddison and Needham 2006; Rix, Harvey and Roberts 2008; Spagna and Gillespie 2008; Vink et al. 2008; Giribet et al. 2010, Miller et al. 2010) and included both mitochondrial and nuclear markers with different degrees of phylogenetic signal. The marker from the mitochondrial genome was the common cytochrome c oxidase subunit 1 (COI) gene. The nuclear genes included two protein-coding genes – histone H3 (H3) and Actin 5C (Act5C) – as well as the small and large subunits of ribosomal RNA genes (18S and 28S, respectively). The GenBank references for each gene sequenced during this study are listed in Appendices 9 and 10. Some taxa for which sequences were available on GenBank were also added in molecular analyses (Appendix 11).

DNA extraction, amplification and sequencing

In the laboratory, a few legs, the carapace or the entire body (usually for mall specimens ≤ 3mm) were used for DNA extraction. DNA samples were extracted with a NucleoSpin® tissue kit (Macherey-Nagel) slightly adapted from the manufacturer's protocol and following the non-destructive method described in Paquin and Vink (2009). The first part of the extraction was performed overnight at 56 °C, and total DNA was then purified the following day. Partial fragments of the mitochondrial (COI) and the four nuclear (H3, Act5C, 18S and 28S) markers were amplified by PCR using the primers specified in Table 1 and 2. PCRs were performed using the QIAGEN Taq DNA Polymerase kit and were carried out in a total volume of 25 µl. The mix PCR contained 0.2 mM of each dNTP, 2.5 µl of PCR buffer 10X, 0.8 µM of each primer, 2.5 mM MgCl2, 5 Units/µl of Qiagen Taq DNA polymerase, 2 µl of extracted DNA and mQ-H2O.

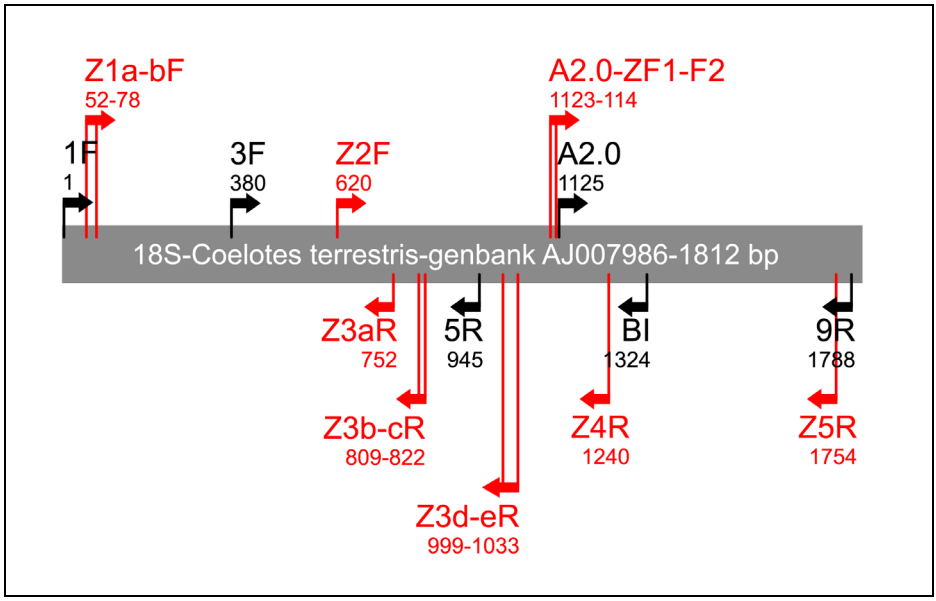


Figure 7. Schematic drawing showing the primers used in this study to amplify and sequence the 18S marker. The relative position and the direction of the primers are depicted on the 1812 bp sequence of *Coelotes terrestris* (Wider, 1834) (GenBank accession number AJ007986). In black, primers known from the literature (see Table 1), in red primers newly designed in this study (see Table 2).

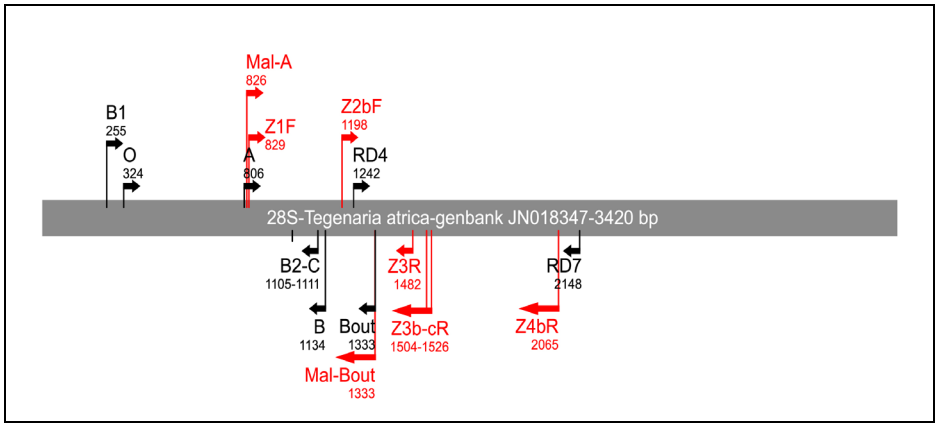


Figure 8. Schematic drawing showing the primers used in this study to amplify and sequence the 28S marker. The relative position and the direction of the primers are depicted on the 3420 bp sequence of *Eratigena atrica* (C. L. Koch, 1843) (GenBank accession number JN018347). In black, primers known from the literature (see Table 1), in red primers newly designed in this study (see table 2).

The presence of amplified target DNA fragments was visually checked on agarose (1.3%) gels. For some difficult samples (those for which the bands appearing on the electrophoresis gel were too weak), the GoTaq and/or DMSO (Dimethyl sulfoxide) were added in the mix PCR (occurred mainly for 18S, 28S and Act5C). The PCR profile comprised an initial denaturation at 94°C for 3' followed by 35 cycles with, per cycle, a denaturation at 94°C for 45" followed by an annealing step of 45" at 48°C. The annealing temperature was sometimes increased up to 52°C to improve the specificity of the primers. The extension step was set at 72°C (1') and with a final extension at 72°C for 10' followed by 10' at 4°C. For some samples for which contaminants (mainly fungi or algae) were sequenced or for samples where multiple bands were observed on the electrophoresis gel, a "touchdown PCR" including three phases were performed to increase the specificity of the amplification. The PCR conditions was as mentioned above except that the annealing steps included 5 cycles at 56°C, then 10 cycles at 52°C and finally by 20 cycles at 48°C. Some target products were amplified and sequenced as two (28S) or three (18S) overlapping sequences that were then assembled in unique consensus sequences in SeqScape v.2.5 (Applied Biosystems). The set of primers known from the literature and detailed in Table 1 was used to amplify and sequence the studied markers. New primers (Table 2) were also designed according to a preliminary alignment of sequences (obtained with the original known primers listed in Table 1) and used on samples of which genetic data was not obtained directly with the original set of primers. Different combinations of primers were tested to amplify and sequence the studied markers (Figs 7 and 8). The positive amplification PCR products were purified using the NucleoFast 96 PCR plate kit (Machery-Nagel). They were then sequenced in both (forward and reverse) directions using the BigDye Terminator V1.1 or 3.1 Cycle Sequencing Kit (Applied Biosystems, Foster City, CA, USA) and finally analyzed with a 16-capillary ABI 3130x Genetic Analyzer (Applied Biosystems, Foster City, CA, USA) host at the RBINS.

Alignment procedures

Analyzed sequences were edited and assembled in SeqScape Software v.2.5 (Applied Biosystems). Each consensus sequence was then blasted in GenBank (BLAST search at http://blast.ncbi.nlm.nih.gov/Blast.cgi) to detect any contamination. Some zodariid and non-zodariid sequences available from GenBank were also included in the multigene alignment (Appendix 11). The non-zodariid taxa do not represent an exhaustive list but they were used as 'multiple outgroups' to better reconstruct the phylogeny of the Zodariidae family, testing its hypothesized monophyly and estimating putative sister group candidate. For each marker, sequences were aligned with MAFFT v.7 implemented online (Katho and Standley 2013) with default settings. The least stringent settings in Gblocks 0.91b (Castresana 2000; Talavera and Castresana 2007. The ambiguous positions in the 18S and 28S alignments were eliminated using Gblocks (Gblocks Server available online at http://molevol.cmima.csic.es/castresana/Gblocks_server.html).

As different sets of primers were used to sequence the COI marker, the resulting sequences were of variable length. Furthermore, sequences taken form GenBank are also variable in length. Gblocks was therefore also used (with the same settings as described above) to trim and refine the COI alignment at both extremities. The Act5C sequences consist of two exon fragments (of around 350 and 420 bp respectively) that enclose an intron of variable length (100-1000 bp). The intron was too variable to be easily aligned and was not included in the analyses. The two Act5C exons were considered as two separate datasets that were defined in such way that any detected stop codons were excluded. A total multigene alignment (COI-H3-Act5C-18S-28S) was created with Mesquite v2.75 (Maddison and Maddison, 2011) by concatenating the MAFFT-Gblocks-curated alignments of the five markers. Only taxa with at least two available sequences were included in the total multigene alignment (see Appendices 9 and 10).

Phylogenetic analyses – molecular data

To account for differences in evolutionary dynamics among sites and sequences, protein coding genes (COI, H3 and Act5C) were partitioned into single codon positions. Models of sequence evolution were evaluated for each partition using PartitionFinder 2 (Lanfear et al. 2016). The analysis was performed with PhyML 3.0 (Gindon et al. 2010), using the greedy algorithm (Lanfear et al. 2012), setting 'branchlengths' to 'linked' and models choice based on the Bayesian Information Criterion (BIC) (Appendix 12).

In this study, the phylogeny of the Zodariidae was mainly inferred from partitioned datasets. However, phylogenetic trees were first constructed for each marker in order to discern their phylogenetic signal among loci, prior to combining the data for a multigene analysis. Therefore, in a first stage, preliminary individuals and multigene analyses were performed (Appendices 13-20) and sequences generating too long branches on the trees or suspected to be too divergent paralogous copies (sequences in bold in Appendices 1 to 3, see also resulting trees in Appendices 14b-17b, 20) were not included in the FINAL multigene analysis. The FINAL multigene alignment comprised 126 taxa and 4944 sites.

Phylogeny reconstructions were evaluated both for each locus and concatenated datasets using Maximum likelihood (ML). To assess the repeatability of results, we also used Bayesian methods (BI) on the multigene datasets to infer the phylogeny and test the robustness of nodes and branches. ML analyses were conducted in GARLI v2.1 (Genetic Algorithm for Rapid Likelihood Inference; Zwickl 2006) using the model specified by PartitionFinder for each partition (Appendix 12). To obtain the ML topology with the best likelihood score, 10 search replicates were ran with the following default setting values changed: streefname = random, attachmentspertaxon = [two

times the number of taxa], genthreshfortopoterm = 100000; scorethreshforterm = 0.001 and significanttopochange = 0.0001. Node supports were assessed from 1000 bootstraps obtained with four independent runs of 250 independent searches, each starting from a random tree.

The following settings were further adjusted to speed up the bootstrapping (*cf.* GARLI manual): genthreshfortopoterm = 10000; significanttopochange = 0.01 and treerejectionthreshold = 20. The discrete gamma distribution of rates across sites was set to 6 categories when applicable. The bootstrap values were then summarized on the best ML tree using SumTree 4.0.0 (part of the DendroPy 4.0.0 package, Sukumaran and Holder, 2010).

BI was evaluated using MrBayes (MB) v3.2.2 (Huelsenbeck and Ronquist 2001, Ronquist and Huelsenbeck 2003, Ronquist et al. 2012) and Phylobayes (PB) (Lartillot et al. 2009). MB analyses were conducted between 10,000,000 to 50,000,000 generations, until it was checked that the standard deviation of split frequencies decreased below 0.01 and the tree search was conducted according to MrBayes defaults (two independent runs each consisting of one cold and three heated MCMC chains). Best-fit models were applied to each partition (see Appendix 12). Parameters were estimated independently for each partition using the following command: unlink statefreq = (all) revmat = (all) shape = (all) pinvar = (all) tratio = (all). The discrete gamma distribution of rates across sites was set to 6 categories when applicable. Convergence diagnostics were also checked with Tracer V1.6 (Rambaut et al. 2014) by examining the effective sample size values (ESS > 200) and to ensure that the Markov chains had reached stationarity. Trees were sampled every 1000th generation and were used to reconstruct a 50% majority rule consensus tree after having discarded the first 25% as burn-in (MB default) (Appendix 18).

BI performed with PB on the multigene alignments were carried out on the CIPRES Science Gateway (Miller et al. 2010b) with as model the CAT profile mixture and GTR (general time reversible) exchange rates. The discrete gamma distribution of rates across sites was set to 6 categories. Tree searches were run with sub-sampling every 10 trees, constant sites removed, the accept discrepancies value of 0.1, a minimum effective size of 300 and a burn-in of 1000. The resulting tree is found in Appendix 19).

Combined analysis

The morphological matrix (153 characters) was incorporated into the multigene alignment (4944 sites), to form a combined DNA-MORPHO dataset comprising 93 taxa (7 are non-Zodariidae and represent the outgroups) and 5097 sites. In the combined phylogenetic analysis, genetic and morphological data were simultaneously analyzed in a probabilistic framework and for this additional partition; data type was set as "standard", both in ML and MB analyses. Tree searches were conducted as described above in "Phylogenetic analyses – molecular data".

Most of the sequenced taxa or species could be morphologically scored. However, for few samples used in the molecular analyses (especially undetermined samples), morphological data were added from the literature and/or based on other taxa. *Lutica* samples (DNA Z096 and Z0256) are juveniles and information on some morphological characters (such as those linked to the genitalia) was based on *Lutica abalonea* Gertsch, 1961 (morphological data obtained from the literature). *Amphiledorus sp.* (DNA Z239) is a sub-adult male and complementary information was obtained from *Amphiledorus balnearius* Jocqué & Bosmans, 2001 (morphological data obtained from the literature) occurring in the same area (see Appendix 1). *Storenomorpha* sp. (DNA Z254) is juvenile and *Storenomorpha arboccoae* Jocqué & Bosmans, 1989 was used to fill gaps in the morphological data (extracted from the literature).

Hermippus cf. *affinis* Strand, 1906 (DNA Z249) is a sub-adult female and complementary morphological data was obtained from the literature and by examining a male specimen in collection (RMCA_ARA_164324). *Asceua lejeunei* (DNA Z029) is a juvenile female and morphological scoring was completed with adult specimens collected at the same locality (RMCA_ARA_239640). *Palfuria* sp. (DNA Z206) is an adult male specimen belonging to an undescribed species and for morphological characters of the female, it was associated with *Palfuria caputlari* Szüts & Jocqué, 2001 (RMCA_ARA_202528) with which it appears closely related. Samples of *Penestomus egazini* (DNA Z282) and *P. prendinii* (DNA Z283) used in the molecular analyses were extracted total DNA products provided Jeremy Miller. Morphological data was mainly obtained from the literature but, at least, the paratype female of P. *egazini* (CAS 9023774, DNA voucher JM8-15) could be examined.

Edition and annotation of trees

Trees were first displayed and drawn in programs such as WINCLADA 1.00.08 (Nixon 1999–2002) or FigTree v1.4.2 (Rambaut 2006–2014) then exported in a vector image format (.emf or .svg) and edited in Inkscape for final publication.

Some explanations are required to read the species labels as depicted in the molecular trees: the first four-letter abbreviation in front of the species name represents the DNA number (arbitrary work numbers). Taxa without such DNA number are those for which sequences were obtained from GenBank. The two last couples of abbreviations after species names represent the location of the specimen used in the analyses. The two-letter code represents the continents or major geographical regions (AF: Africa; AS: Asia; EU: Europe; NA: North America; SA: South America; OC: Oceania). The three-letter abbreviation represents the country codes defined by the International Organization for Standardization (ISO 3166-1 alpha-3).

RESULTS

The present section reports the results of all analyses performed in this study. Phylogenetic relationships will be discussed in the discussion section whereas taxonomic actions and diagnosis of groups will be discussed in the section 'Systematics'.

Three main tree topologies will be considered for the discussion of the phylogenetic results and for the diagnosis of the taxa: the tree generated by the parsimony analysis under implied weights with concavity constant of k = 4 (Fig. 9 and Appendix 7), the ML tree obtained from the multigene analysis (Figs 10-14), and the ML tree obtained from the combined analysis (Fig. 15).

Phylogenetic analyses

Morphology-based analysis

We choose to illustrate here the result for K=4 because it was the most congruent with the results from the molecular analyses. The parsimony analysis carried out in TNT with implied weighting (k=4) provided 5 most parsimonious trees of length 1041 (best score 60.59795, with CI = 21 and RI = 77). The majority rule consensus tree of length 1043 (best score 60.68108, CI = 22 and RI = 77) is shown in Fig. 9 (overview) and detailed in Appendix 7. All characters were informative, and 73 unambiguous character state changes are non-homoplasic (see Appendix 7). Ambiguous character optimizations can be solved in order to favor reversal or secondary loss over convergence and the number of non-homoplasic characters is then higher (= 99, option 'fast optimization' in WINCLADA). The result of the parsimony analysis with all characters equally weighted is shown in Appendix 6 and the morphological Bayesian tree is shown in Appendix 8.

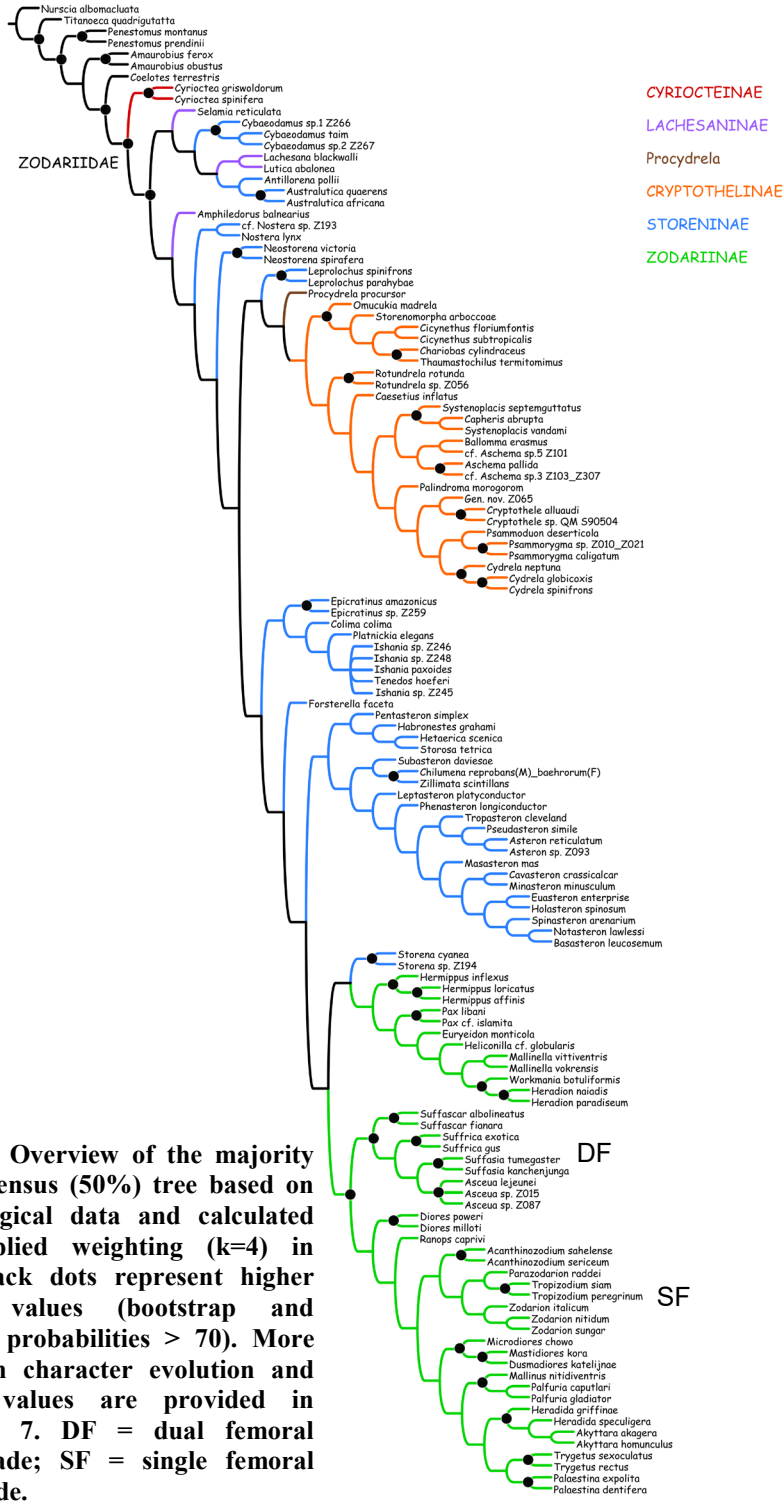


Figure 9. Overview of the majority rule consensus (50%) tree based on morphological data and calculated with implied weighting (k=4) in TNT. Black dots represent higher support values (bootstrap and posterior probabilities > 70). More details on character evolution and support values are provided in Appendix 7. DF = dual femoral organ clade; SF = single femoral organ clade.

Molecular-based analyses

Sequence data and alignments

We were able to generate a total of 515 DNA sequences (GenBank accession number listed in Appendices 9 and 10) from 120 taxa, among which 113 Zodariidae represented by 59 known genera and one unknown genera from Mont Nimba in Guinea (= DNA Z065). Amplification and sequencing results were highly successful, especially for COI (98 % of all samples) and H3 (94 %), but also for 18S (86 %) and 28S (87 %). The newly designed primers only allowed to retrieve a few lacking sequences in general, except for the last part of the 18S fragment that was almost entirely obtained with the new couple of primer 18S-A2.0-ZF2/18S-Z5R (see Table 2). Actin 5C was the marker with the lowest amplification success (barely 50% of the samples yielded a sequence). However, due to time and financial constraints, we could not try subsequent optimized PCR reactions nor try or design new primers for this gene region.

Multigene phylogenetic analysis

This analysis is based on the FINAL multigene dataset comprising 126 taxa and 4944 sites, of which 1454 are informative. The best ML tree obtained with GARLI on the multigene alignment was used to summarize the support values of nodes (ML bootstrap and posterior probabilities) resulting from the different phylogenetic analyses performed in this study (Figs 10-14). Bayesian inference (BI) executed with MrBayes (MB) and Phylobayes (PB) provided similar topologies and is also given in Appendices 18 and 19 respectively. Fig. 10 provides an overall view of the phylogeny whereas Figs 11-14 detail each recognized group in this study.

Trees resulted from ML analyses on each marker and analyses with supposed paralogous sequences are presented in Appendices 13-17 and 20.

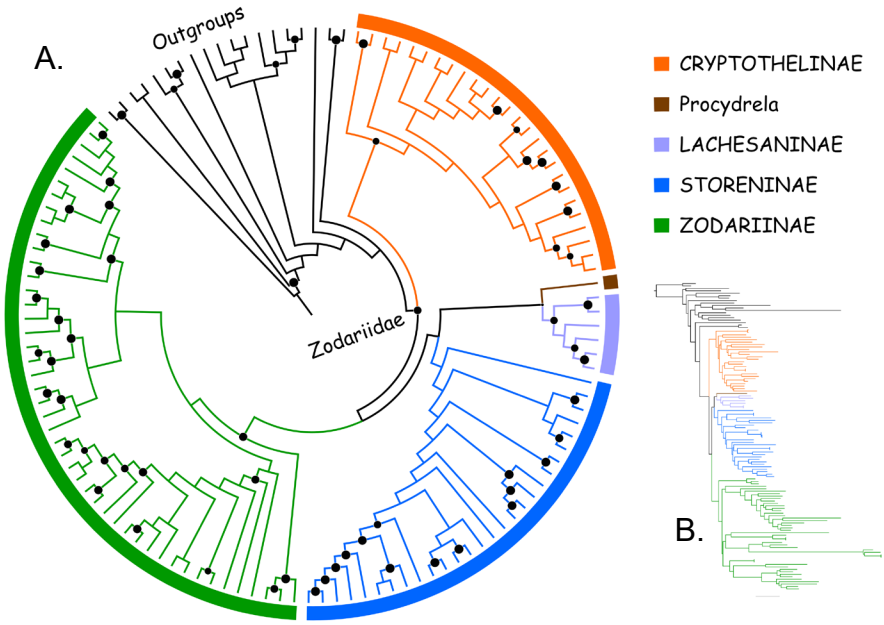


Figure 10A-B. Overview of Zodariidae phylogeny reconstructions, highlighting the different recognized groups. A. Circular cladogram representing the best ML tree is shown, resulting from the analysis on the FINAL multigene dataset performed with GARLI under the models specified in Appendix 12. The branch lengths have been modified to facilitate the visualization of relationships between subfamilies within Zodariidae. Black dots represent higher support values (ML bootstrap > 70). B. Backbone ML tree showing branch lengths. Details of subfamily relationships and node supports are depicted on Figs 11 to 14.

Combined phylogenetic analysis

The results of the phylogeny reconstruction based on the combined DNA-MORPHO dataset are depicted on Fig. 14 and represent the total evidence tree on which we mainly base our evolutionary hypothesis. The ML and MB analyses provided similar topologies and the support values obtained with ML in GARLI and MB in MrBayes are summarized on the best ML tree (Fig. 15).

Phylogenetic relationships

All morphological (Fig. 9 and Appendix 7), multigene (Figs 10-14) and combined (Fig. 15) phylogenetic analyses strongly supported the monophyly of the Zodariidae. The sister group relationship of Penestomidae and Zodariidae is well supported in both multigene (Fig. 11) and combined analyses (Fig. 15A) (although only strongly supported by ML in the multigene analysis). In the morphological analysis, Penestomidae are not placed sister to the Zodariidae as suggested by molecular analyses (cf. Discussion for more details on the affinities with Penestomidae). The deeper relationships between the other outgroup taxa are mainly unsolved, especially in the multigene analysis.

The combined and the multigene trees highlight at least 4 major groups that can be defined as: Lachesaninae, Cryptothelinae, Storeninae and Zodariinae. All these groups are supported both by ML and BI (except Storeninae that are only supported by the latter inference) (Figs 13-14 and 15B, C). The morphological data alone failed to resolve such groups, except the Cryptothelinae, which are however mainly supported by MB (Appendices 7 and 8). In addition, the Cyriocteinae (absent from molecular analyses) have a sister-relationship to of other zodariids with good support.

Inside Cryptothelinae, a clade including some elongate zodariids (i.e. *Cicynethus*, *Chariobas* and *Thaumastochilus*) appears consistently supported in all phylogenetic analyses (moderately supported in the morphological tree (see Appendix 7), but with strong support in the multigene (Fig. 12) and combined (Fig. 15B) trees). The relationship of *Procydrela procursor* as sister to Cryptothelinae, was recovered but unsupported in the morphological analysis. Similarly, its placement was not stable in the multigene analysis, differing between the ML (Figs 10 and 13), MB (Appendix 18) and PB analyses (Appendix 19). However, in the combined analysis, only MB supports its placement as sister group to Cryptothelinae (Fig 15B).

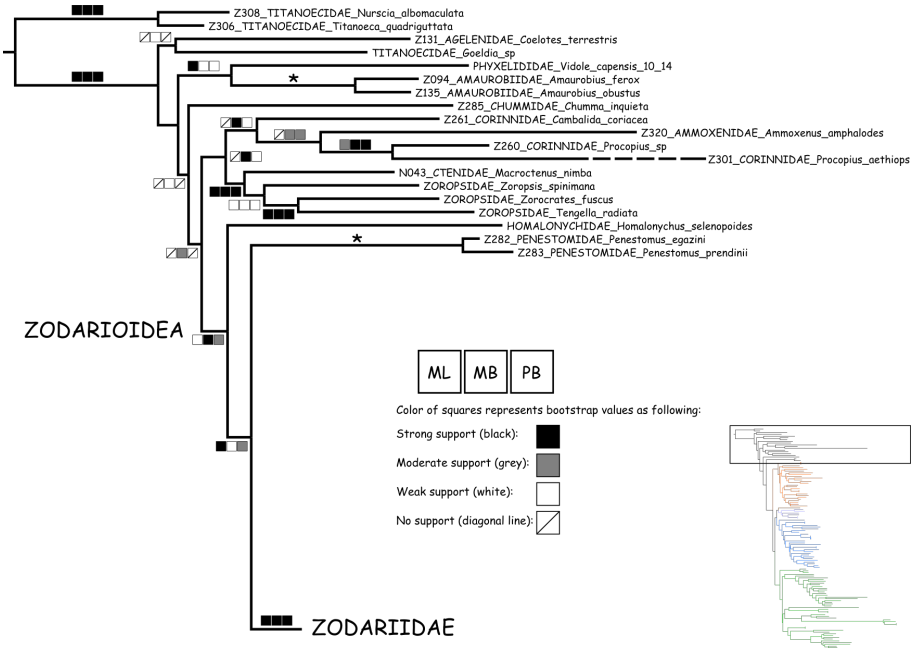


Figure 11. Details of the Fig. 10 with a close up on the outgroups and some representatives of the Zodarioidea (*i.e.* Homalonychidae and Penestomidae). Support values obtained from the different phylogenetic methods run on the FINAL multigene molecular dataset are summarized here on the best ML tree. Squares at nodes indicate the analysis method (ML, maximum likelihood; MB, Bayesian Inference performed with MrBayes; PB, Bayesian Inference performed with PhyloBayes). Color of squares represents support values (ML bootstrap; MB and PB posterior probabilities): strong support in black (ML ≥ 0.70; MB, PB ≥ 0.95), moderate support in grey (0.60 ≤ ML < 0.70; 0.75 ≤ MB, PB < 0.95), weak support in white (0.50 < ML <0.60; 0.50 < MB < 0.75) and no support (or when nodes on the ML tree are not recovered on the MB or PB trees) in white with diagonal line. No squares are shown at nodes without any support. Stars indicate very strong supports (values above 99 and 0.99) in all the analyses.

The clade defining the Storeninae occurs both in multigene and combined analyses. However, only the BI gives high support for its monophyly (Figs 13 and 15B). Among Storeninae, most relationships remain unsupported, with the exception however of an "Australasian clade" (including *Storena*, *Nostera*, *Neostorena*, *Asteron*, *Habronestes* and *Forsterella*) appearing supportedly monophyletic in the multigene and combined phylogenetic analyses (Figs 13 and 15B).

The multigene and the combined analyses also strongly supported the monophyly of the Zodariinae (Figs 10, 14 and 15C). The internal relationship inside this group is relatively well resolved, especially in the combined analysis (Fig. 15C). It further highlights three monophyletic sub-groups, for which the well-supported femoral organ clade (DF + SF) is sister to a clade here called "*Mallinella* clade" (which include *Hermippus*, *Pax*, *Heradion*, *Heliconilla* and *Mallinella*), also well supported in this analysis. The multigene analysis, however, does not recover the same strong results, providing only good supports for the SF clade. The only groups well supported by morphological data is the femoral organ clade (DF + SF) and the DF alone (Fig. 9 and Appendix 7).

DISCUSSION

Phylogenetic relationships

The Outgroups

As the relationships among the outgroups were not the primary focus of the present study, the sample of outgroups taxa does not represent an exhaustive list of both morphological and molecular analyses. However, but it allowed at least to test the proposed monophyly of the Zodariidae and their subgroups and to determine the phylogenetic placement of the different studied taxa and groups. Among the outgroup taxa, one can note a robust clade including Ctenidae and Zoropsidae (Fig. 11). The remaining deeper relationships between the other outgroup taxa remain unsolved.

The Zodarioidae

The Zodarioidea (Fig. 11), which also include the Homalonychidae and Penestomidae, received moderate support. Homalonychidae were missing from our morphological analysis. However the three families Homalonychidae, Penestomidae and Zodariidae, although looking

very dissimilar morphologically, share the singular disposition of the major ampullate gland spigots (char. 132–1), which are encircled by the piriform glands spigots instead of being placed on a marginal field (Ramírez et al. 2014, figs 4D-F, 5A-F). In our morphological analysis, the Penestomidae are not placed sister to the Zodariidae as suggested by molecular analyses (Miller et al. 2010a; Dimitrov et al. 2017; Wheeler et al. 2017; this study). However, another analysis in which the deactivation (in an additional analysis) of characters linked to the presence of a cribellum (char. 152 & 153) gave a similar topology but with Penestomidae splitting of sister to the Zodariidae (see Appendix 7).

It was shown that the cribellum is a synapomorphy for all Araneomorphae that has been subject to multiple losses (or to a reduced, non-functional colulus) in many spider lineages (Todd et al. 2009; Miller et al. 2010a; Garrison et al. 2016; Dimitrov et al. 2017; Wheeler et al. 2017). In our analysis, the presence of the cribellum (and the calamistrum) is symplesiomorphic (as it is present in the outgroups Titanoecidae) and the loss of the cribellum (152–1) appears as a non-homoplasic synapomorphy for *Coelotes* (Agelenidae) and the Zodariidae in our analysis (Appendix 7). However, although most of the Agelenidae are ecribellate, there are a few representatives of this family that still have a cribellum, such as *Tamgrinia* Lehtinen, 1967 (Miller et al. 2010a; Wheeler et al. 2017). The loss of the cribellum is therefore undoubtedly not homologous and evolved independently in *Coelotes* (Agelenidae) and the Zodariidae. These characters evidently undermine the support for the placement of Penestomidae as sister to Zodariids in our analysis. When they are excluded from the analysis, we obtain Penestomidae sister to the Zodariidae (see Appendix 7), both characterized by the toothless unpaired tarsal claw (char. 71–1, Appendix 5: Figs 6C-G) and, with fast optimization, the ALS with the major ampullate gland spigots situated in the center of the spinnerets (char. 132–1).

As mentioned above, the Homalonichidae is also usually considered as part of the Zodarioidae (*e.g.* Wunderlich 2004; Moradmand et al. 2014; Garrison et al. 2016) even though it often has a variable position in recent phylogenetic analyses (e.g. Miller et al. 2010a; Wheeler et al. 2017; Fernández et al. 2018; Shao and Li 2018). In our multigene analyses, *Homalonychus selenopoides* was always recovered as sister to the remaining zodarioids, even though only supported by MB. However, the number and spreading of outgroup taxa is not sufficient to really discuss its phylogenetic placement here.

The Zodariidae

The parsimony analysis and all analyses based on multigene and combined datasets strongly recovered the monophyly of the Zodariidae (Figs 9-15), even when supposedly problematic sequences were not removed from the analysis (see Appendix 20).

The morphological analysis characterizes the Zodariidae by the combination of five non-homoplasic characters and several homoplasic characters (Appendix 7). The most conspicuous characters shared by all known Zodariidae are the endites devoid of a serrula (48–1) and the legs with a tibial process (85–1). The tarsal claw teeth standing on the lateral side of the claw facing each other (Char 74–1, 2 and 75–1, 2, Appendix 5: Figs 6D-H) was considered a synapomorphy for almost all Zodariidae (Jocqué 1991a): Cyrioctea is the only zodariid taxon that has the plesiomorphic state on all legs (the teeth are ventrally implemented: 74–0, 75–0). However, this character also occurs in other dionychan spider families (e.g. Homalonychidae, Liocranidae, Ammoxenidae, Trochanteriidae, …) (Ramírez 2014). In a few zodariid taxa the row is oblique and the most proximal teeth stand in the axis of the claw (74–1 and 75–1, see Appendix 5: Figs 5E, F). The Penestomidae, however, have a zodariid-like conformation on the anterior legs (74–2), and a plesiomorphic state on the posterior ones (75–0) (Ramírez et al. 2014, figs 8D-E).

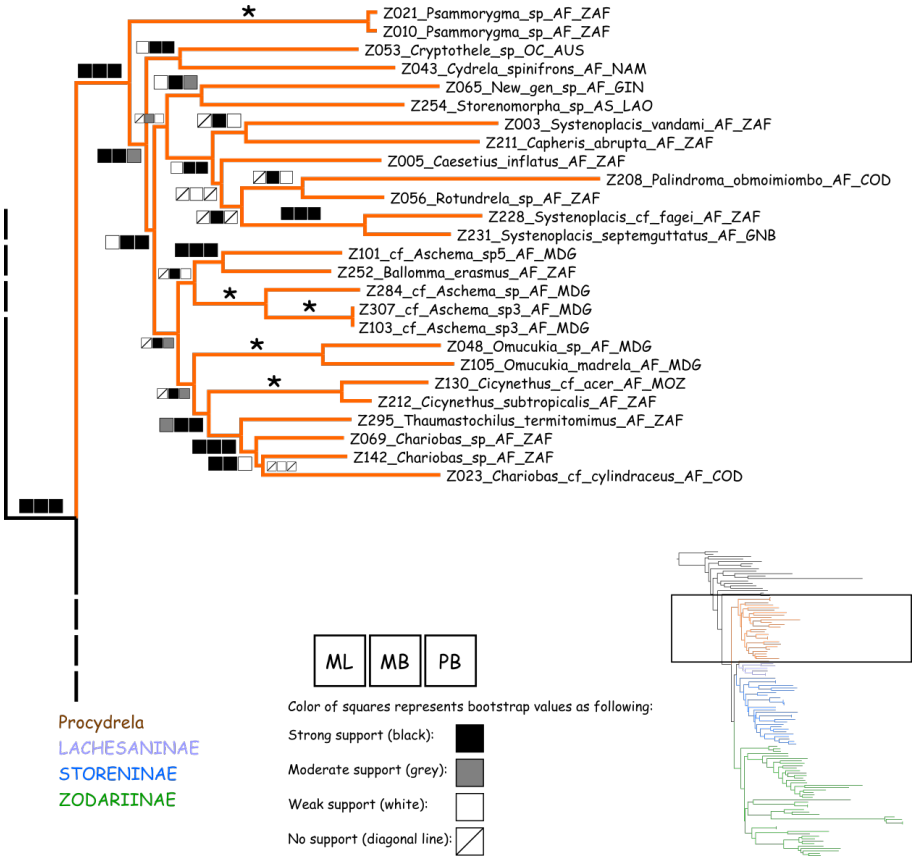


Figure 12. Details of the Fig. 10 with a close up on the Cryptothelinae (orange clade). Support values obtained from the different phylogenetic methods run on the FINAL multigene molecular dataset are summarized here on the best ML tree. Squares at nodes indicate the analysis method (ML, maximum likelihood; MB, Bayesian Inference performed with MrBayes; PB, Bayesian Inference performed with PhyloBayes). Color of squares represents support values (ML bootstrap; MB and PB posterior probabilities): strong support in black (ML ≥ 0.70; MB, PB ≥ 0.95), moderate support in grey (0.60 ≤ ML < 0.70; 0.75 ≤ MB, PB < 0.95), weak support in white (0.50 < ML <0.60; 0.50 < MB < 0.75) and no support (or when nodes on the ML tree are not recovered on the MB or PB trees) in white with diagonal line. No squares are shown at nodes without any support. Stars indicate very strong supports (values above 99 and 0.99) in all the analyses.

The Cyriocteinae

The Cyriocteinae were lacking in our molecular analysis. This clade is represented in the morphological analysis by *Cyrioctea griswoldorum* Platnick & Jocqué, 1992 and *C. spinifera* (Nicolet, 1849) (type species of the genus). In the parsimony analysis (Fig. 9, Appendix 7), the representatives of the subfamily Cyriocteinae appear sister to all remaining zodariids as predicted by previous studies (Platnick 1986; Platnick and Griffin 1988; Jocqué 1991a; Ramírez et al. 2014; Wheeler et al. 2017).

The Cyriocteinae still share several plesiomorphic characters such as the ventral position of the teeth on the paired tarsal claw (74–0, 75–0) (Appendix 5: Fig. 6C) or the non-reduced posterior median spinnerets (PMS) (129–0; 130–0). The PMS are not modified in *Cyrioctea* species whereas they are often strongly reduced, sometimes fused with the posterior lateral spinnerets (PLS) (Jocqué & Baert 2005, figs. 2-5) in other zodariids. Another plesiomorphic character in common with the outgroups is the presence of cheliceral teeth in *Cyrioctea*, which is assumed to be usually absent in zodariids (Jocqué 1991a, Ramírez et al. 2014). However the distribution, across the phylogenetic tree, of the characters linked to the presence of teeth or teeth-like modifications on the chelicerae (chars 53 to 57), is far from being clear. The presence of several teeth on the retromargin (54–0) is common in the outgroup taxa whereas most Zodariidae have no teeth (54–2). The presence of only one tooth on the retromargin (54–1) is found in Cyriocteinae, *Procydrela*, some Storeninae (*Australutica africana*, *Epicratinus*, *Ischania*, *Platnickia* and *Tenedos*) and some representatives of the DF clade in the Zodariinae (i.e. *Asceua*, *Suffasia* and *Suffrica*). The distribution of char. 55 (chelicerae with teeth on promargin) across the tree is even more complex. The presence of at least 3 teeth on the promargin (55–0) is again common in the outgroup taxa but also in the Cyriocteinae.

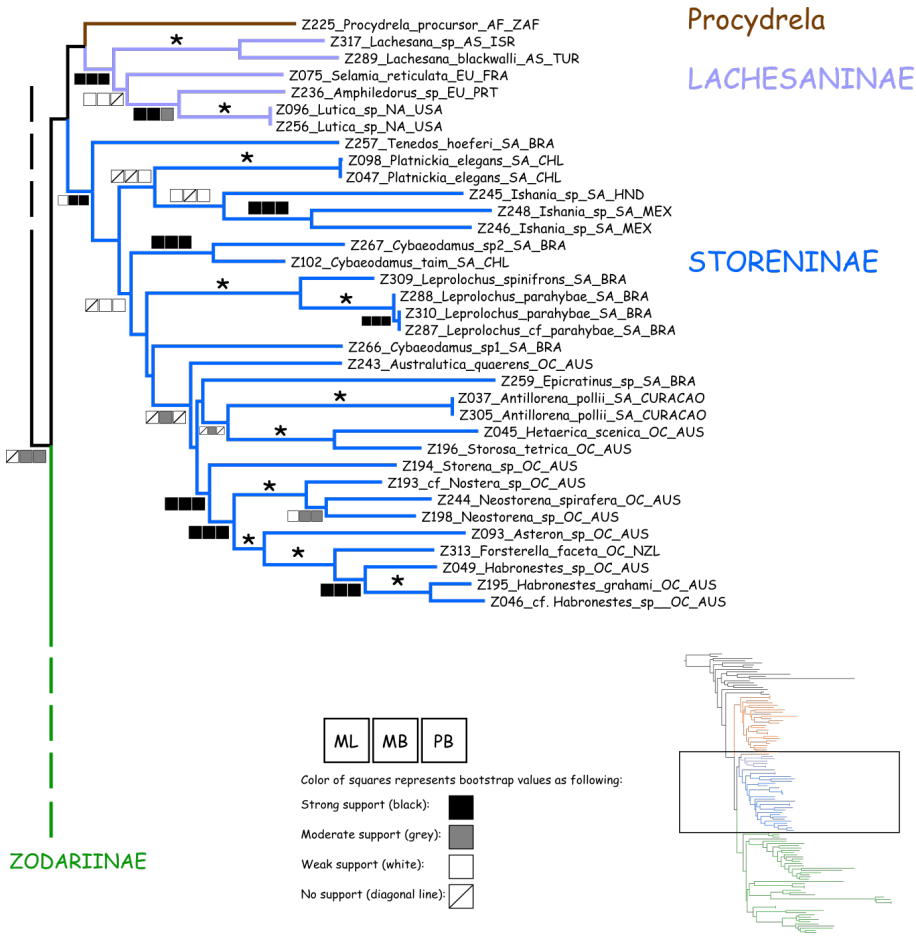


Figure 13. Details of the Fig. 10 with a close up on the *Procydrela* (brown branch), Lachesaninae (violet clade) and Storeninae (blue clade). Support values obtained from the different phylogenetic methods run on the FINAL multigene molecular dataset are summarized here on the best ML tree. Squares at nodes indicate the analysis method (ML, maximum likelihood; MB, Bayesian Inference performed with MrBayes; PB, Bayesian Inference performed with PhyloBayes). Color of squares represents support values (ML bootstrap; MB and PB posterior probabilities): strong support in black (ML ≥ 0.70; MB, PB ≥ 0.95), moderate support in grey (0.60 ≤ ML < 0.70; 0.75 ≤ MB, PB < 0.95), weak support in white (0.50 < ML <0.60; 0.50 < MB, PB < 0.75) and no support (or when nodes on the ML tree are not recovered on the MB or PB trees) in white with diagonal line. No squares are shown at nodes without any support. Stars indicate very strong supports (values above 99 and 0.99) in all the analyses.

Several Zodariidae have no teeth on the promargin (55–3) but the presence of one or two teeth (55–1, 55–2) is also found in many zodariid taxa in the Lachesaninae (only absent in *Lutica*), *Procydrela*, Storeninae and Zodariinae. In the Cryptothelinae, however, only *Cryptothele* was observed to possess two small teeth on the promargin (Appendix 5: Figs 4G, H), which were probably overlooked by Ramírez et al. 2014. Indeed, those teeth are almost translucent and thus practically invisible under stereomicroscope but obvious with SEM.

The Lachesaninae

In the Cladistic analysis of Jocqué (1991), the Lachesaninae included *Antillorena* Jocqué, 1991, *Lachesana* and *Lutica*. Later, Jocqué (1995a) also proposed *Australutica* Jocqué, 1995 to be part of the Lachesaninae. According to our molecular analyses, the Lachesaninae also include *Selamia* and *Amphiledorus*, but *Antillorena* and *Australutica* fall into the Storeninae (Figs 13 and 15B). In our morphological analysis (Fig. 9, Appendix 7), the Lachesaninae are not recovered although all the representatives are somewhat scattered near the base of the tree, along with some Storeninae such as *Cybaeodamus* Mello-Leitão, 1938, *Antillorena*, *Australutica*, *Nostera* Jocqué, 1991 and *Neostorena* Rainbow, 1914. The Lachesaninae are recovered both in the multigene and in the combined analyses with strong supports (Figs 13 and 15B). The relationships of this clade remain uncertain due to unsupported lower nodes in molecular analyses (Fig. 13). One can note however that with the addition of morphological data, in the combined analysis (Fig. 15B), Lachesaninae is placed is sister to all remaining zodariid subfamilies (but only supported by MB).

***Procydrela* Jocqué, 1999**

The genus *Procydrela* Jocqué, 1999 includes two species known from South Africa. *Procydrela procursor* Jocqué, 1999 was the only species present in our analyses.

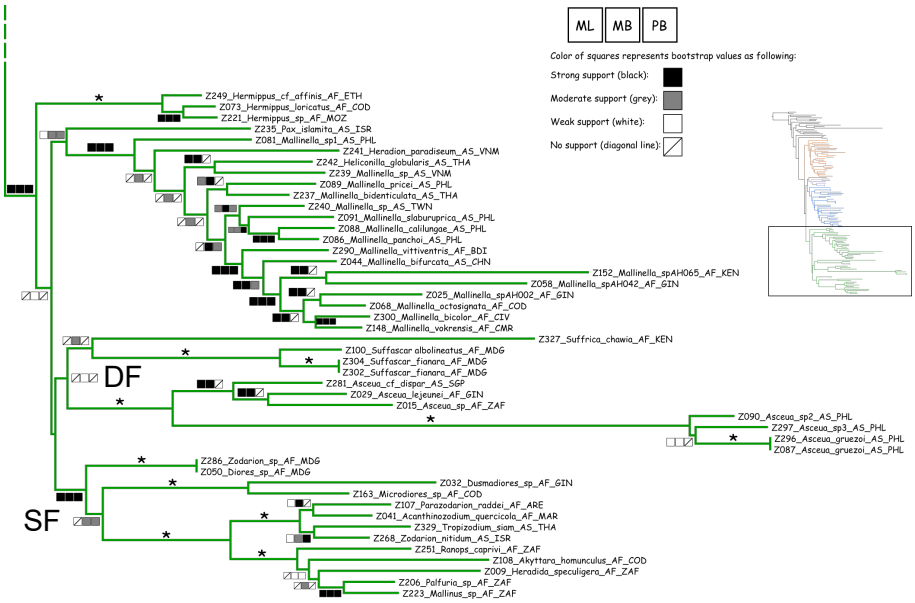


Figure 14. Details of the Fig. 10 with a close up on the Zodariinae (green clade). Support values obtained from the different phylogenetic methods run on the FINAL multigene molecular dataset are summarized here on the best ML tree. Squares at nodes indicate the analysis method (ML, maximum likelihood; MB, Bayesian Inference performed with MrBayes; PB, Bayesian Inference performed with PhyloBayes). Color of squares represents support values (ML bootstrap; MB and PB posterior probabilities): strong support in black (ML ≥ 0.70; MB, PB ≥ 0.95), moderate support in grey (0.60 ≤ ML < 0.70; 0.75 ≤ MB, PB < 0.95), weak support in white (0.50 < ML <0.60; 0.50 < MB < 0.75) and no support (or when nodes on the ML tree are not recovered on the MB or PB trees) in white with diagonal line. No squares are shown at nodes without any support. Stars indicate very strong supports (values above 99 and 0.99) in all the analyses. DF = dual femoral organ clade; SF = single femoral organ clade.

In its description, Jocqué (1999) suggested that *Procydrela* might be the sister-group of the "Cydrelinae plus Storenomorphinae" (= Cryptothelinae in this study). This assumption is retrieved in the combined analysis (Fig. 15B), although only supported by MB. However its phylogenetic position could not be determined with certainty in the multigene analyses. For these reasons, as it cannot be attributed to any group, it may be necessary to place it in a group of its own.

The Cryptothelinae

The Cryptothelinae are strongly supported by molecular (both multigene and combined) analyses (Figs 9, 11, 14). They are also recovered by morphological data (Fig. 9, Appendix 7) but mainly supported by bayesian inference. Surprisingly, the Cryptothelinae are only characterized by the combination of several homoplasic features (see Appendix 7).

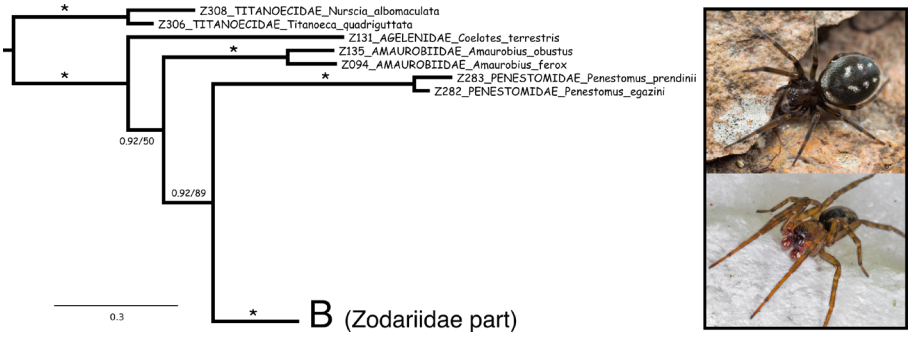
Cryptothele L. Koch, 1872

As firstly suggested by Simon (1893), then by Jocqué and Dippenaar-Schoeman (2007) and, with more evidence, by the recent studies of Ramírez et al. (2014) Jocqué and Henrard (2015b) and Wheeler et al. (2017), the deep inclusion of *Cryptothele* in the Cryptothelinae is also solidly confirmed by our study.

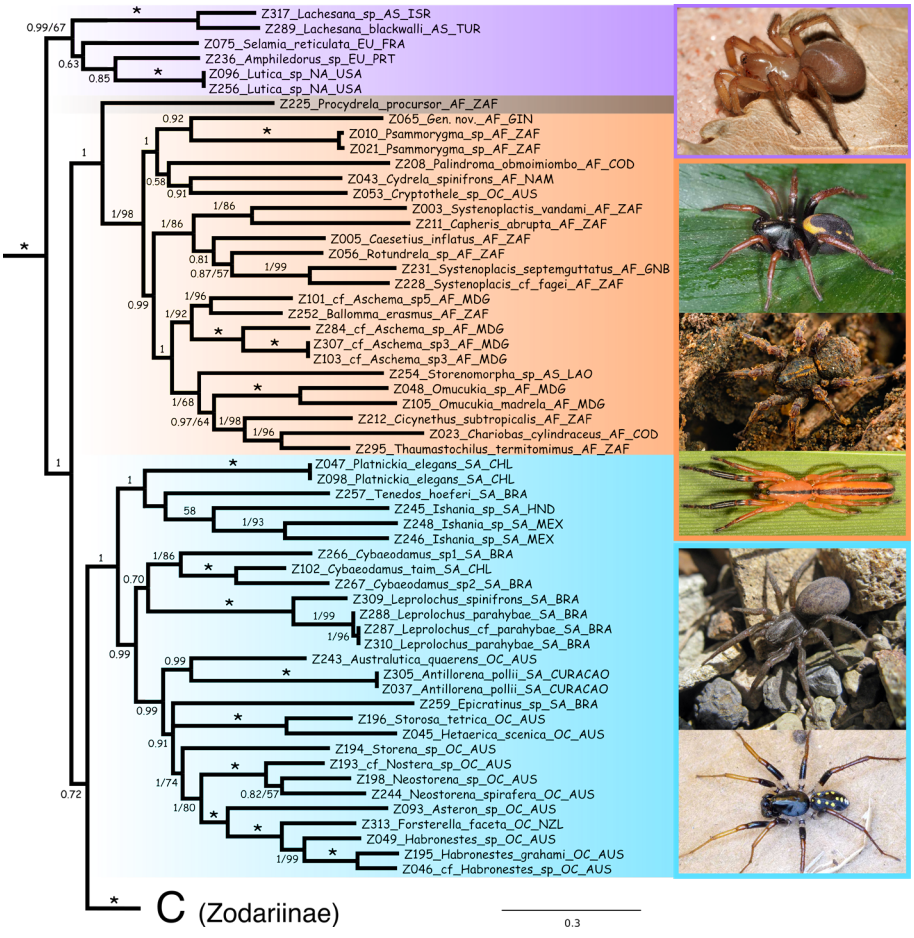
The 'Storenomorphinae'

In the analysis of Jocqué (1991a), the 'Cydrelinae' are sister to the 'Storenomorphinae', which include *Chariobas* Simon, 1893, *Cicynethus* Simon, 1910, *Omucukia* Koçak & Kemal, 2008, *Storenomorpha* Simon, 1884 and *Thaumastochilus* Simon, 1897. In our morphological analysis and combined analysis, this clade is recovered. However, interestingly, in the multigene analysis, *Storenomorpha* is excluded from this group (but still in the Cryptothelinae). Only a smaller clade of three elongate taxa (*Cicynethus*, *Chariobas* and *Thaumastochilus*) is well supported in all the three main phylogenetic analyses (morphology, multigene and combined) for which *Omucukia* appears sister (however, much less supported in general). As the 'Storenomorphinae' appear paraphyletic in the molecular analyses and fall into the Cryptothelinae, we suggest that Storenomorphinae are fused with Cryptothelinae.

A.


Z308_TITANOECIDAE_Nurscia_albomaculata
Z306_TITANOECIDAE_Titanoeca_quadriguttata
Z131_AGELENIDAE_Coelotes_terrestris
Z135_AMAUROBIIDAE_Amaurobius_obustus
Z094_AMAUROBIIDAE_Amaurobius_ferox
Z283_PENESTOMIDAE_Penestomus_prendinii
Z282_PENESTOMIDAE_Penestomus_egazini
0.92/50
0.92/89
0.3
B (Zodariidae part)

B.


Z317_Lachesana_sp_AS_ISR
Z289_Lachesana_blackwalli_AS_TUR
Z075_Selamia_reticulata_EU_FRA
Z236_Amphiledorus_sp_EU_PRT
Z096_Lutica_sp_NA_USA
Z256_Lutica_sp_NA_USA
Z225_Procydrela_procursor_AF_ZAF
Z065_Gen. nov._AF_GIN
Z010_Psammorygma_sp_AF_ZAF
Z021_Psammorygma_sp_AF_ZAF
Z208_Palindroma_obmoimiombo_AF_COD
Z043_Cydrela_spinifrons_AF_NAM
Z053_Cryptothele_sp_OC_AUS
Z003_Systenoplactis_vandami_AF_ZAF
Z211_Capheris_abrupta_AF_ZAF
Z005_Caesetius_inflatus_AF_ZAF
Z056_Rotundrela_sp_AF_ZAF
Z231_Systenoplacis_septemguttatus_AF_GNB
Z228_Systenoplacis_cf_fagei_AF_ZAF
Z101_cf_Aschema_sp5_AF_MDG
Z252_Ballomma_erasmus_AF_ZAF
Z284_cf_Aschema_sp_AF_MDG
Z307_cf_Aschema_sp3_AF_MDG
Z103_cf_Aschema_sp3_AF_MDG
Z254_Storenomorpha_sp_AS_LAO
Z048_Omucukia_sp_AF_MDG
Z105_Omucukia_madrela_AF_MDG
Z212_Cicynethus_subtropicalis_AF_ZAF
Z023_Chariobas_cylindraceus_AF_COD
Z295_Thaumastochilus_termitomimus_AF_ZAF
Z047_Platnickia_elegans_SA_CHL
Z098_Platnickia_elegans_SA_CHL
Z257_Tenedos_hoeferi_SA_BRA
Z245_Ishania_sp_SA_HND
Z248_Ishania_sp_SA_MEX
Z246_Ishania_sp_SA_MEX
Z266_Cybaeodamus_sp1_SA_BRA
Z102_Cybaeodamus_taim_SA_CHL
Z267_Cybaeodamus_sp2_SA_BRA
Z309_Leprolochus_spinifrons_SA_BRA
Z288_Leprolochus_parahybae_SA_BRA
Z287_Leprolochus_cf_parahybae_SA_BRA
Z310_Leprolochus_parahybae_SA_BRA
Z243_Australutica_quaerens_OC_AUS
Z305_Antillorena_pollii_SA_CURACAO
Z037_Antillorena_pollii_SA_CURACAO
Z259_Epicratinus_sp_SA_BRA
Z196_Storosa_tetrica_OC_AUS
Z045_Hetaerica_scenica_OC_AUS
Z194_Storena_sp_OC_AUS
Z193_cf_Nostera_sp_OC_AUS
Z198_Neostorena_sp_OC_AUS
Z244_Neostorena_spirafera_OC_AUS
Z093_Asteron_sp_OC_AUS
Z313_Forsterella_faceta_OC_NZL
Z049_Habronestes_sp_OC_AUS
Z195_Habronestes_grahami_OC_AUS
Z046_cf_Habronestes_sp_OC_AUS
C (Zodariinae)
0.3

C.

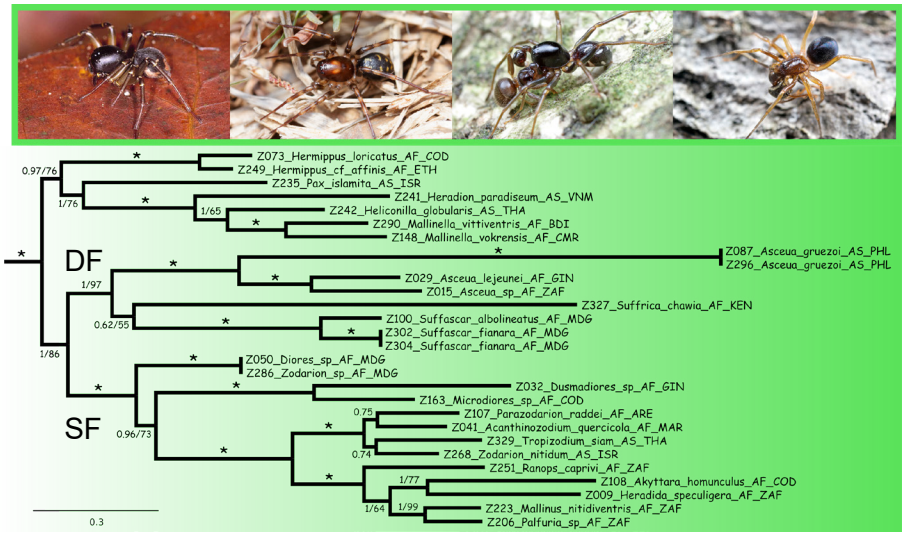


Figure 15A-C. Phylogeny reconstruction of the Zodariidae based on the combined DNA-MORPHO dataset. Support values were obtained with different phylogenetic methods (MB/ML) and are summarized here on the best ML tree. Values below 50/0.50 are not shown and stars indicate strong supports (≤ 0.99/99) in both ML and MB analyses. A. Part of the tree including the outgroups. Photos (from top to bottom): *Nurscia albomaculata* and *Amaurobius obustus* (both © Arnaud Henrard) B. Part of the tree including the Lachesaninae (purple clade), *Procydrela procursor* (in brown), Cryptothelinae (orange clade) and Storeninae (blue clade). Photos (from top to bottom): *Lachesana blackwalli* (© Rudolf Macek), *Psammorygma sp.* (© Martín Ramírez), *Cryptothele sp.* (© Nicky Bay), *Chariobas sp.* (© Peter Webb), *Cybaeodamus taim* (© Cristian Grismado), *Habronestes hunti* (© Robert Whyte). B. Zodariinae part in (green). DF = dual femoral organ clade; SF = single femoral organ clade. Photos (from left to right): *Hermippus* sp. (© Martín Ramírez), *Mallinella sp.* (© Arnaud Henrard), *Asceua japonica* (© Takashi Komatsu) and *Zodarion nigrifemur* (© Arnaud Henrard).

The Storeninae

The Storeninae are re-established and redefined from Jocqué (1992) and its composition is strongly changed as compared to the that in Jocqué 1991a, including some ex-Lachesaninae (*i.e. Antillorena* and *Australutica*) and excluding several taxa such as *Hermippus*, *Pax*, *Mallinella* and close relatives, which are now in the Zodariinae.

Although recovered both in each multigene and combined molecular analysis (Figs 10, 13 and 15B), the monophyly the Storeninae is supported by Bayesian methods only (Figs 13 and 15B). Again, inside the subfamily, most of the nodes are poorly, if not, supported. The only clade supported (strongly) in the multigene and combined analyses and by both ML and BI includes some Australasian representatives (i.e. *Storena* Walckenaer, 1805, *Nostera* Jocqué, 1991, *Neostorena* Rainbow, 1914, *Asteron* Jocqué, 1991, *Habronestes* L. Koch, 1872 and *Forsterella* Jocqué, 1991). In the morphological analysis the Storeninae are not recovered, with representatives scattered over the trees, except a groups of exclusively Australian taxa (unfortunately most were not available for molecular analyses) (Fig. 9 and Appendix 7). As a consequence, the Storeninae are morphologically hard to define. Jocqué (1991a) characterized Storeninae mainly by the presence of typical chisel-shaped setae (Char. 76–2) composing a preening brush at the apex of the posterior metatarsi (Appendix 5: Figs 6K, L). The Storeninae represent a paraphyletic group in the cladistic analysis of Jocqué (1991a), excluding the Zodariinae, characterized by the presence of a femoral organ (Appendix 5: Figs 7A-H, 8G) on the legs and supposedly devoid of chisel-shaped setae. But later, some taxa were found to possess both femoral organs and chisel-shaped setae and, as a consequence, the Storeninae were fused into the Zodariinae (Jocqué 1992). More recently, other taxa were discovered to share the combination of chisel-shaped setae and femoral organs (Henrard and Jocqué 2015, 2017a). It was therefore suggested to diagnose Storeninae on the presence of preening brushes with chisel-shaped setae in combination with the absence of femoral organs (Henrard and Jocqué 2017a). However the character, *i.e.* the ventral metatarsal preening brushes with chisel-shaped setae, has several reversals (76–0) inside the subfamily and the derived state (76–2) is also present in some Zodariinae (ex-Storeninae) such as the DF clade, *Hermippus*, *Pax*, *Mallinella* and other close relatives.

The Zodariinae

The Zodariinae subfamily *sensu* Jocqué (1991a) was mainly characterized by the presence of a femoral gland although many other autapomorphies characterize this clade (see also Appendix 7 "SF clade" and Henrard and Jocqué 2017a). The multigene and the combined analyses (Figs 10, 14 and 15C) strongly supported the Zodariinae, which are redefined to include representatives of the typical femoral organ clade (SF) and some ex-Storeninae (taxa of the DF clade, *Hermippus*, *Pax*, *Mallinella* and close relatives). The Act5c and 28S ML analyses recovered the Zodariinae as well, although no supports are provided for these individual genes.

The relationships inside the subfamily are far from being resolved with molecular data only. In the Zodariinae, three sub-groups are recognized and are strongly supported by the combined analysis (Fig. 15C): the DF clade, the SF clade and one other sub-group, here called "Mallinella-clade", appearing sister to DF + SF and which include *Hermippus*, *Pax*, *Heradion*, *Heliconilla* and *Mallinella* (also *Workmania* judging from the morphological results, Fig. 9 and Appendix 7).

Although the morphological analysis alone did not support the monophyly of the subfamily, it recovered the three sub-groups mentioned above. One can also note the representatives of the genus *Storena* that fall sister to the "*Mallinella* clade" in the morphological analysis. This is not totally surprising: although now well defined (Jocqué 1991a, Jocqué and Baehr 1992) by the pitted shield on the dorsum of the abdomen (119–1), the name *Storena* has been used for a plead of roughly similar spiders (WSC 2018). *Storena* shares several homoplasic features with some zodariine taxa such as the typical triangular extensions of the sternum margins (42–1) and, to cite the most relevant, the presence of promarginal teeth on the chelicerae (55–2), the spination on the legs (94–1), and some characteristics on the spinnerets (128–0, 130–0 and 131–1).

However, molecules clearly support its deep inclusion in the Storeninae and its affinity with other Australasian taxa (Figs 13, 15B, Appendix 15).

Evolution of the femoral organ clades

Morphological data recovered the sister group relationship of the DF and SF clades and their monophyly (Fig. 9, Appendix 7), as previously obtained by Henrard and Jocqué (2017a). However, surprisingly, the multigene analyses do not support the monophyly of the femoral organ clade (i.e. DF + SF), and only SF clade is strongly supported (Fig. 14). Given the morphological evidence (see Appendix 7), it is also surprising that the DF clade is so weakly supported (Fig. 13) in the multigene analysis.

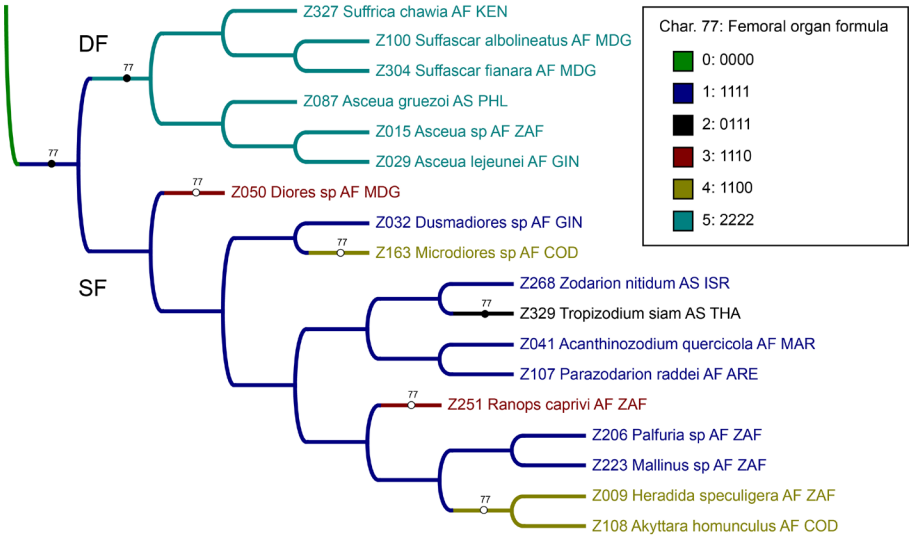


Figure 16. Mapping the character 77 on the femoral organs tree (based on the combined DNA-MORPHO tree shown on Fig. 11). The femoral organ formula indicates the number of femoral organ present on each leg. Character numbers (fast optimization) are placed above the circles and coloration indicates the state change (cf. the box). Black circles indicate non-homoplasic synapomorphies and white circles indicate homoplasic changes. DF = dual femoral organ clade; SF = single femoral organ clade.

Nevertheless, when the morphological data are joined to the molecular data in the combined analysis, there is considerably stronger support for the sister group relationship of the DF and SF and the monophyly of DF (Fig. 14). With molecular data only, it is not possible to infer whether femoral organs appeared once or evolved several times independently. The femoral organ is a quite complex structure (Jocqué and Billen 1987; Jocqué 1988b; Pekár and Šobotník 2007) implying the development of a gland on an unusual location for a spider. It is therefore very unlikely that this character has developed twice (Jocqué 1991a). However, even based on the morphological and combined analysis, the evolution of the femoral organ and its complexity (chars 77 to 84) remain ambiguous and not completely resolved. Indeed, for characters linked to the presence of the femoral organ on legs (chars 77 to 81), which represent important features to define the SF and DF clades, there are several possible solutions for the appearance of a state. Therefore, the state change cannot be inferred unambiguously and these characters do not appear on the cladogram (see Appendix 7) despite their exclusivity to the group.

However, if ambiguous characters are optimized in order to avoid convergence (= 'fast optimization' in WINCLADA) one can suggests the early appearance of a single femoral gland, which later evolved towards a double gland in the DF clade. The Fig. 16 shows the evolution of the femoral organ formula represented by char. 77 (the character was "mapped" on the combined tree using WINCLADA). The presence of the femoral organ on legs and its complexity (chars 71 to 84; see also Jocqué and Billen 1987) is variable within the SF clade whereas is quite simple and invariably dual on each leg in the DF clade (see also Henrard and Jocqué 2015; 2017).

Among the SF taxa, the most common combination is 1111 (77–1), a single gland on each leg is present in 9 zodariine genera (*Acanthinozodium* Denis, 1966, *Dusmadiores* Jocqué, 1987, *Mallinus* Simon, 1893, *Mastidiores* Jocqué, 1987, *Palaestina* O. Pickard-Cambridge, 1872, *Palfuria* Simon, 1910, *Parazodarion* Ovtchinnikov, Ahmad & Gurko, 2009, *Trygetus* Simon, 1882and *Zodarion* Walckenaer, 1826). Our results (Fig. 16) suggest that the other combinations were independently derived from state 1 (77–1). The lost of femoral organ on legs I (combination 0111, char. 77–2) is an autapomorphy for *Tropizodium* Jocqué & Churchill, 2005. The loss of the femoral organ on legs IV (combination 1110, char 77–3) appears to have evolved twice, in *Diores* Simon, 1893 and *Ranops* Jocqué, 1991 (Fig. 16). The loss of the femoral organ on legs III and IV (formula 1100, char. 77–4) also appears to be derived independently form the combination 1111 (77–1) in *Microdiores* Jocqué, 1987 and *Akyttara* Jocqué, 1987 + *Heradida* Simon, 1893.

The Zodariinae, and especially the femoral organ clade (SF), are often regarded as the most derived members of the family (Jocqué 1991a, Pekár et al. 2012a; Pekár et al. 2013; Pekár and Toft 2015; Haddad et al. 2019) and most of the species in it have a strongly specialized diet. However, not all representatives of the Zodariinae seem to be compulsory ant- or termite-eaters. Indeed, *Mallinella* for instance appears more generalist than previously thought (Pekár 2012a): several undescribed African taxa were observed to feed also on flies or crickets in laboratory conditions (A. Henrard, pers. observations). Moreover, the evolution towards ant- or termite-eating specialization appear to have evolved independently in other taxa such as in *Leprolochus birabeni* Mello-Leitão, 1942, a stenophagous ant-eating specialist (Pompozzi et al. 2018) and in *Diores* spp. (Jocqué and Dippenaar-Schoeman 1992) and *Cryptothele* (Abraham 1924; Koh 1989; Ramírez et al. 2014), which are both termites-predators.

SYSTEMATICS

In the following sections, we characterize as much as possible the groupings based on the results obtained by the combined (Fig. 15) and the multigene analyses (Figs 10-14). Morphological characters that can support for certain recovered groupings are provided by the parsimony analysis with concavity K = 4 (Appendix 7, list of characters in Appendix 5). A distribution map for each group is also provided.

Zodarioidea

The Zodarioidea includes the three families Homalonychidae, Penestomidae and Zodariidae. Although looking very dissimilar morphologically, they share a few characteristics such as the central position of the major ampullate gland spigots surrounded by the piriform glands spigots on the ALS (char. 132–1) (see Jocqué & Baert 2005, fig. 6; Ramírez 2014, figs 119C, D; Ramírez et al. 2014, figs 4D-F, 5A-F). Furthermore, the invagination of the major ampullate gland spigots, although only partially invaginated in Homalonychus, Penestomus and in a few zodariids, may represent a putative synapomorphy for this group (Ramírez et al. 2014). For some other shared characters, the group appears fairly heterogeneous. While Homalonychidae lacks tarsal claw teeth, Penestomidae has a zodariid-like (except Cyrioctea) conformation on the anterior legs, and ventral teeth on the posterior ones. Although it is present in the Penestomidae, Homalonychidae and Zodariidae do not have a serrula on the endites (48–1).

Zodariidae

According to the morphological analysis (Appendix 7) the Zodariidae are characterized by the combination of five non-homoplasic characters (33–1, 48–1, 85–1, 93–2 and, in fast optimization, 110–1).

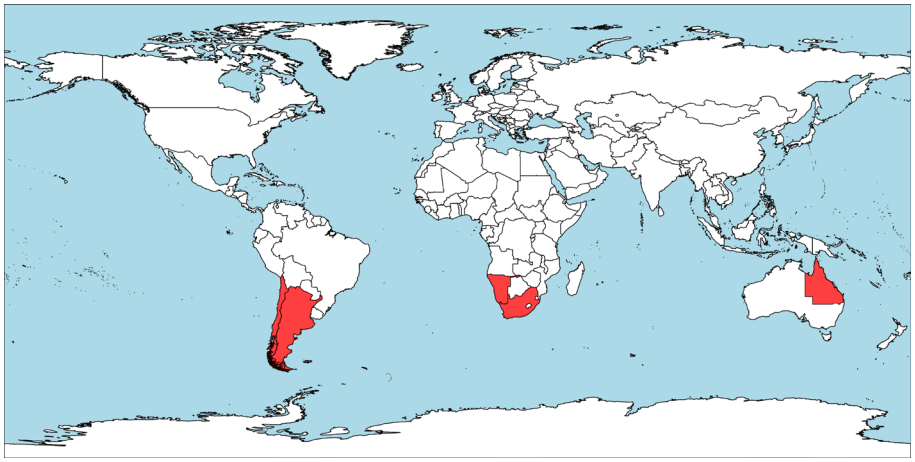


Figure 17. Distribution of the Cyriocteinae (based on the WSC 2018).

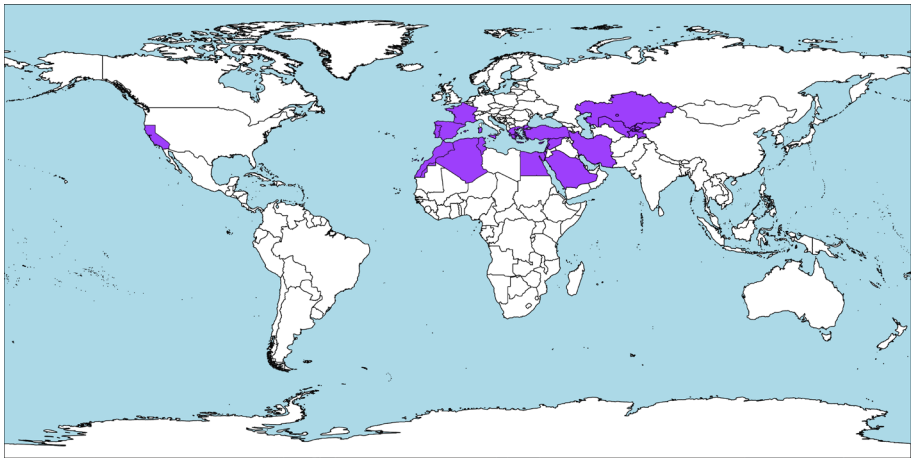


Figure 18. Distribution of the Lachesaninae (based on the WSC 2018).

The most conspicuous characters shared by all known Zodariidae are the endites devoid of a serrula (48–1) and the legs with a tibial process (85–1). The family is further characterized by several homoplasic characters (18–1, 19–1, 51–1, 66–1, 71–1, 124–1 and in fast optimization 1–0 and 54–1). According to Ramírez et al. (2014), the complete invagination of the major ampullate field is a potential synapomorphy of zodariids even though the invagination is partial in Penestomidae and in few zodariids (e.g. *Cryptothele*, *Mallinella* and *Zodarion*) or may be ambiguous, between two states (partial/complete) in other taxa (*Cydrela*, *Tenedos*).

Cyriocteinae

The subfamily includes the genus *Cyrioctea* Simon, 1889 only. Unfortunately *Cyrioctea* could not be part of our molecular analyses. This clade is represented in the parsimony analysis by *Cyrioctea griswoldorum* Platnick & Jocqué, 1992 and *C. spinifera* (Nicolet, 1849) (type species of the genus). The Cyriocteinae are clearly characterized by the transverse row of spines in the eye region between AER and PER (char. 35–1, Fig. 1B and Appendix 5: Figs 2I, K) and also by the widely separated AME (24–1).

They are also characterized by the combination of homoplasic characters (6–1, 22–1, 24–1, 27–1, 36–2, 37–1, 120–1, 126–1 and also 25–0 under fast optimization). *Cyrioctea* is known to have a typical Gondwanaland distribution pattern (Jocqué 1993; 2008; 2013; Murphy and Roberts 2015), with representatives restricted to the southern parts of the continents Africa, Australia and South America (Figure 17).

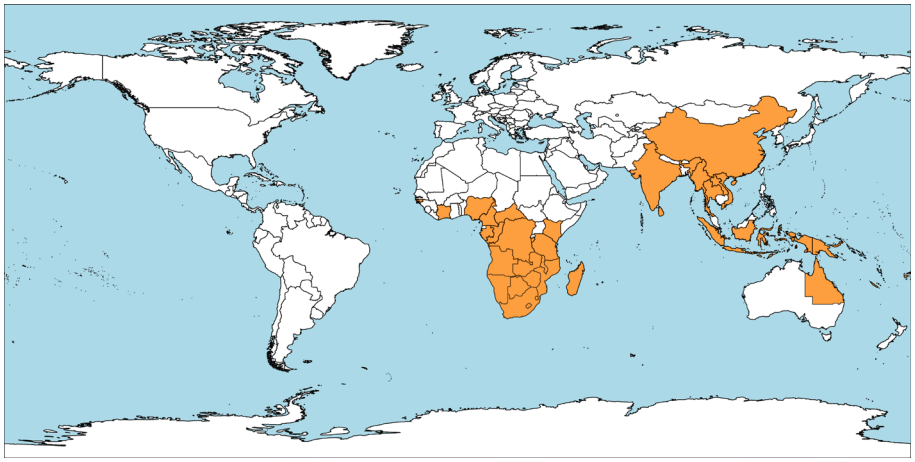


Figure 19. Distribution of the Cryptothelinae (based on the WSC 2018).

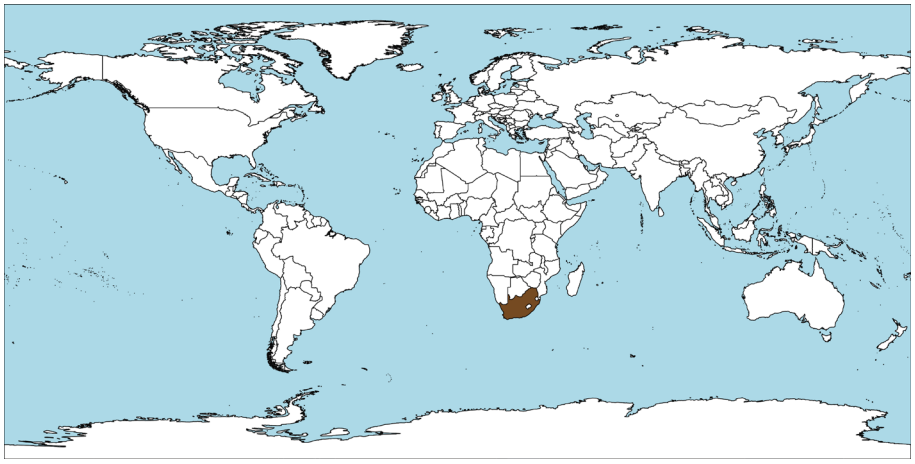


Figure 20. Distribution of the Cryptothelinae (based on the WSC 2018).

Lachesaninae

This subfamily contains the genera *Amphiledorus* Jocqué & Bosmans, 2001, *Lachesana* Strand, 1932, *Lutica* Marx, 1891, and *Selamia* Simon, 1873. Species of this subfamily are mainly distributed around the Mediterranean and in Central Asia (*Amphiledorus*, *Lachesana* and *Selamia*) (Fig. 18). *Lutica* is the only native representative of the Zodariidae in the USA and is restricted to the Californian coast and nearby islands.

Cryptothelinae

Although strongly supported in the phylogenetic analyses, the Cryptothelinae are only characterized by the combination of several homoplasic features (17–2, 26–0, 27–2, 44–1, 47–1, 97–1, 122–0 and in fast optimization 25–0, 76–1, 126–0, 144–0, 145–0) (see Appendix 7). Most of the Cryptothelinae are characterized (together with *Procydrela*) by the thick spines or thorns present on the palp of both sexes. This subfamily includes the genera *Aschema* Jocqué, 1991, *Ballomma* Jocqué & Henrard, 2015, *Caesetius* Simon, 1893, *Capheris* Simon, 1893, *Chariobas* Simon, 1893, *Cicynethus* Simon, 1910, *Cryptothele* L. Koch, 1872, *Cydrela* Thorell, 1873, *Palindroma* Jocqué & Henrard, 2015, *Psammoduon* Jocqué, 1991, *Psammorygma* Jocqué, 1991, *Rotundrela* Jocqué, 1999, *Storenomorpha* Simon, 1884, *Systenoplacis* Simon, 1907 and *Thaumastochilus* Simon, 1897.

The Cryptothelinae occur in Africa below the Sahel and from India to Australia (Fig. 19).

Procydrela *Jocqué, 1999*

The genus *Procydrela* Jocqué, 1999 includes two species occurring in South Africa (Fig. 20): *Procydrela limacola* Jocqué, 1999 and *Procydrela procursor* Jocqué, 1999.

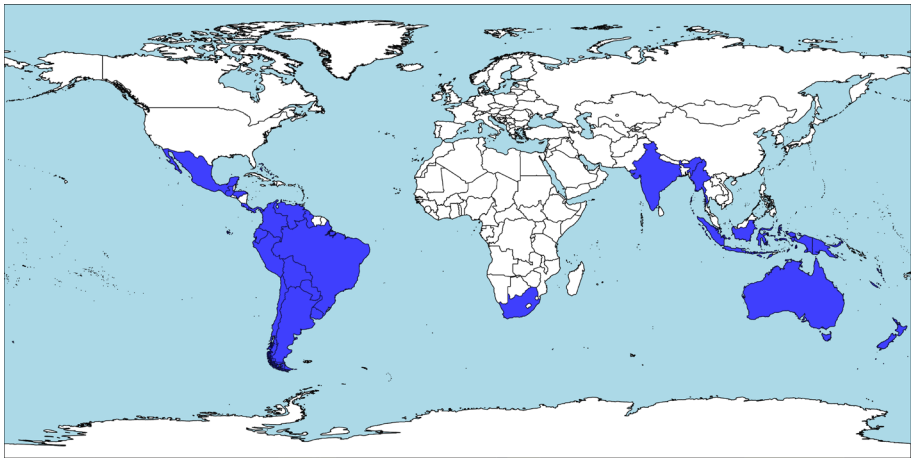


Figure 21. Distribution of the Storeninae (based on the WSC 2018).

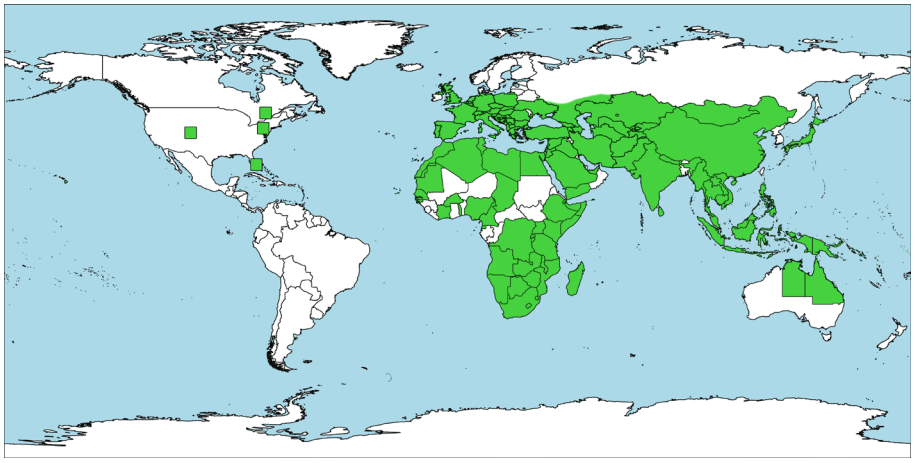


Figure 22. Distribution of the Zodariinae (based on the WSC 2018).). Squares represent isolated records of few *Zodarion* species, supposedly introduced in the USA and Canada.

The morphological analysis characterizes *P. procursor* with numerous homoplasic characters (see Appendix 19). The phylogenetic position of *Procydrela* could not be determined with certainty in the molecular analyses. However, in the combined analysis (Fig. 15) and in the morphological analysis with implied weighting (k=4) (Fig. 9 and Appendix 7), it falls sister to the Cryptothelinae, with which it shares some homoplasies (13-1; 107-2 and in fast optimization 143-2). The most conspicuous feature are the thick spines or thorns present on the palp of both sexes (107-2 and 143-2), which are supposed to be adaptations for digging (reversed to state 1 in the 'Storenomorphinae' sensu Jocqué 1991a).

Storeninae

The Storeninae are re-established from Jocqué (1992) and its composition has strongly changed as compared to the that in Jocqué 1991a. Although the monophyly is recovered both in each multigene and combined phylogenetic analysis (supported by Bayesian methods only, Figs 13 and 15B) most of the nodes are poorly, if not, supported inside the subfamily. Similarly, the Storeninae are no recovered in the morphological analysis and with representatives mainly scattered over the trees (Fig. 9 and Appendix 7). As a consequence, the Storeninae are morphologically hard to define.

This subfamily includes the genera *Antillorena* Jocqué, 1991, *Asteron* Jocqué, 1991, *Australutica* Jocqué, 1995, *Basasteron* Baehr, 2003, *Cavasteron* Baehr & Jocqué, 2000, *Chilumena* Jocqué, 1995, *Colima* Jocqué & Baert, 2005, *Cybaeodamus* Mello-Leitão, 1938, *Epicratinus* Jocqué & Baert, 2005, *Euasteron* Baehr, 2003, *Forsterella* Jocqué, 1991, *Habronestes* L. Koch, 1872, *Hetaerica* Rainbow, 1916, *Holasteron* Baehr, 2004, *Ishania* Chamberlin, 1925, *Leprolochus* Simon, 1893, *Leptasteron* Baehr & Jocqué, 2001, *Masasteron* Baehr, 2004, *Minasteron* Baehr & Jocqué, 2000, *Neostorena* Rainbow, 1914, *Nostera* Jocqué, 1991, *Nosterella* Baehr & Jocqué, 2017, *Notasteron* Baehr, 2005, *Pentasteron* Baehr & Jocqué, 2001, *Phenasteron* Baehr

& Jocqué, 2001, *Platnickia* Jocqué, 1991, *Pseudasteron* Jocqué & Baehr, 2001, *Spinasteron* Baehr, 2003, *Storena* Walckenaer, 1805, *Storosa* Jocqué, 1991, *Subasteron* Baehr & Jocqué, 2001, *Tenedos* O. Pickard-Cambridge, 1897, *Tropasteron* Baehr, 2003 and *Zillimata* Jocqué, 1995.

The Storeninae occur in Central and South America, in South Africa (*Australutica* only) and from India to Australia where they reach their highest diversity (Fig. 21).

Zodariinae

Two to three main groups characterize the Zodariinae. The femoral organ clade (DF + SF) is clearly defined by the presence of femoral glands (and several other homoplasie characters) whereas the "*Mallinella* clade" is much less easier to characterize, sharing few homoplasies (Appendix 7). The Zodariinae includes the taxa *Acanthinozodium* Denis, 1966, *Akyttara* Jocqué, 1987, *Asceua* Thorell, 1887, *Diores* Simon, 1893, *Dusmadiores* Jocqué, 1987, *Euryeidon* Dankittipakul & Jocqué, 2004, *Heliconilla* Dankittipakul, Jocqué & Singtripop, 2012, *Heradida* Simon, 1893, *Heradion* Dankittipakul & Jocqué, 2004, *Hermippus* Simon, 1893, *Leviola* Miller, 1970, *Malayozodarion* Ono & Hashim, 2008, *Mallinella* Strand, 1906, *Mallinus* Simon, 1893, *Mastidiores* Jocqué, 1987, *Microdiores* Jocqué, 1987, *Palaestina* O. Pickard-Cambridge, 1872, *Palfuria* Simon, 1910, *Parazodarion* Ovtchinnikov, Ahmad & Gurko, 2009, *Pax* Levy, 1990, *Ranops* Jocqué, 1991, *Suffascar* Henrard & Jocqué, 2017, *Suffasia* Jocqué, 1991, *Suffrica* Henrard & Jocqué, 2015, *Tropizodium* Jocqué & Churchill, 2005, *Trygetus* Simon, 1882, *Workmania* Dankittipakul, Jocqué & Singtripop, 2012, *Zodariellum* Andreeva & Tyschchenko, 1968 and *Zodarion* Walckenaer, 1826.

The Zodariinae are widely distributed, being absent from America (except few introduced species) and from northern Palearctic and only reached the Northern Territory and Queensland in Australia (Fig. 22).

CONCLUSION

The results of the analyses performed in this study showed general consistency for some of the groups obtained by the different methods. Despite the low resolution inside some clades and at deeper nodes, the multigene approach supported the same clades and the same relations among them in the different probabilistic analyses used. In our morphological analysis, the lack of support for the proposed groups, and the few synapomorphies it revealed, may be the consequence of too much noise in the matrix, resulting from the multiple homoplasies among the characters. However, the combined approach analyzing the integrated molecular and morphological matrices, yielded stronger results in terms of support and consistency and provided stable solutions for the problems formulated in the introduction.

The findings of this study provide additional evidence corroborating the monophyly of the Zodariidae family, which turns out to be sister to the Penestomidae, a family that shows only superficial morphological similarity.

The main subfamilies are re-established in great lines but needed redelimitation. *Procydrela procursor* Jocqué, 1999 could not be assigned to any subfamily and future analyses will tell whether it must be placed in a group of its own.

The evolution of the femoral organ and its complexity remain ambiguous and not fully resolved in the molecular analysis. However, it seems unlikely that this character has developed independently twice. The combined analysis may suggest an early appearance of a single femoral gland (of formula 1111), which later evolved towards a double gland in the dual femoral organ clade (formula 2222). The other combinations in the single femoral organ clade would have independently evolved from the formula 1.

APPENDICES

The appendices 1-20 are provided separately on CD-ROM for the ease of lecture.

CHAPTER V

GENERAL DISCUSSION

TAXONOMIC ISSUES

During preliminary analyses and interpretations of the first trees, I faced certain difficulties explaining some phylogenetic results. For some taxa, the place on the cladograms was puzzling, considering the unexpected and at first glance unexplainable affinities. Actually, I discovered that several samples were initially simply wrongly identified. When I discovered that, I started to check thoroughly all the available specimens morphologically, to be sure that samples I received were correctly identified. Not less than seven samples had problems with the identification! Taxonomic issues were solved with the examination of good literature and, when possible, by comparison with type specimens in collection. The latter point is of particular importance and the necessity of preserved specimens as vouchers for taxonomy, for which I strongly plead, is currently vividly debated (e.g. Dubois and Nemésio 2007; Ceriaco et al. 2016; Rogers et al. 2017) as a reaction against photography-based taxonomy (e.g. Marschall et al. 2015; Pape et al. 2016; Garraffoni and Freitas 2017). Modern taxonomy and systematics use a variety of methods, including textual differential diagnoses and descriptions, morphometrics, accurate illustrations, stacked photographs, SEM pictures, Micro-CT representations, as well as a wide range of molecular data (Kropf et al 2019). These different methods have to be used as complementary rather than exchangeable.

Some taxonomic errors were due to the use of Juveniles. For instance, the tube with collection number "RMCA_ARA_217634" included one male correctly identified as *Rotundrela rotunda* Jocqué, 1999. The tube also contained one juvenile supposed conspecific as they were collected together by sifting the litter from a transitional Eucalyptus/Fynbos vegetation in South Africa. In order to preserve the integrity of the male, the use of the juvenile was preferred and received the label DNA Z228 for the molecular analyses.

However, superficial examination of the specimen had actually led to a misidentification of this juvenile. The use of another *Rotundrela* male (DNA Z056) belonging to an undescribed species (however morphologically strongly related to the type species and the correctly identified male RMCA_ARA_217634) showed, in all DNA based trees, no affinities with the juvenile DNA Z228. Re-examination of the latter with the stereomicroscope confirmed (note that it is rarely possible with juvenile spiders) the molecular result suggesting a match with *Systenoplacis* cf. *fagei*. Indeed, a female individual (DNA Z230, for which only the COI sequence was obtained), correctly identified as *Systenoplacis fagei* (Lawrence, 1937) and collected from the same place as the juvenile DNA Z228, proved to have a COI sequence quasi identical to that juvenile. Other similar examples of identification errors included several samples received from the Australian Museum. For instance, it is most probably the case for the sample DNA Z046 (also a juvenile) firstly identified as "*Pentasteron simplex*" (see Appendix 1), which actually falls inside the *Habronestes* clade having strong affinities with DNA Z195, i.e. *Habronestes grahami* Baehr, 2003 (Figs 10, 13, 15B, Appendices 13-20). These cases strongly highlight the importance of reciprocal illumination between morphological and molecular results.

CHARACTER MATRIX AND CODING: WHERE ARE THE SYNAPOMORPHIES ?

Building the morphological matrix (Appendices 4 and 5) was quite demanding and time consuming, but not as much as the molecular part (lab work, generate the sequences, process and analyze bioinformatics). One might think that the higher degree of subjectivity in morphology (this point is discussed below) render the molecular processes more rigorous. However, becoming familiar with the morphology of the species and the groups under study is extremely important to understand the data and interpret the results.

Whereas I was convinced of its taxonomic importance for sciences, I decided, in collaboration with my supervisor Rudy Jocqué, to undertake the description of some unknown zodariid taxa prior to the publication of phylogenies, in order to document some remarkable combinations of features that have not been observed in spiders so far (Henrard and Jocqué 2015; Jocqué and Henrard 2015a; 2015b; 2015c). These studies in the fields of taxonomy and systematics provide important additions to science in general. Indeed, without taxonomical identities, phylogenetic trees are impoverished in the sense that they add little to the understanding of relationships (Wilson 2004; Wheeler 2004; Korf 2005; Agnarsson and Kuntner 2007).

Our matrix comprises almost twice as many characters as that of Jocqué (1991a). The number increased from 79 to 153, which is not surprising considering that since then, 37 genera were added to the Zodariidae (WSC 2018). However, the construction of matrices that are dominated by similarities may be problematic because sometimes homology is uncertain, which invalidates the character choice (Platnick 2016). Good examples are characters associated to leg spines: it is hardly possible to homologize individual leg spines. Without such individual homologies, observations about leg spines are unlikely to contribute real synapomorphies. Our morphology-based tree has revealed widespread patterns of homoplasy among the taxonomic characters of zodariids, generating very few synapomorphies (see Appendix 7). Character optimization resolving ambiguities (in our case in favor of secondary loss over convergence) may reveal more synapomorphies. However, it was demonstrated that neither of them consistently minimize parallel gain of complex traits, the choice being therefore subjective (Agnarsson and Miller 2008). The patterns of character evolution appear not always clear and homology of characters, assumptions formulated prior to the analyses, is not always guaranteed.

On the other hand, some apparently homoplasic characters may have an important contribution more locally in the tree, stabilizing small clades for which the character is relevant. Characters linked to the relative distance between each eyes are a good example in this respect (Chars 21–29). Evidently, it is only at the outcome of an analysis (e.g. a tree) that convergences or homoplasies are discovered and meaningful.

Coding the characters is therefore often a tricky matter (see Strong 1999). I encountered some ambiguous difficulties coding characters for morphological analyses. The choice of a character and the coding of its different forms (i.e. character state) in the matrix are always reasoned but also subject to subjective interpretation, which may result in different results between authors. For many characters I was faced to differences of opinion with my supervisor R. Jocqué. In such cases we only arrived at a consensus after lengthy discussions. We faced the same problem during the study of Afrotropical Ctenidae (Henrard and Jocqué 2017), for which the morphological matrix was based on a previous analysis by other authors (Polotow and Brescovit, 2014). Platnick (l.c.) maintains that "our job, as systematists, is to find the synapomorphies that support every node in the cladogram of life". In our morphological analysis, the lack of definition of the proposed groups and the few synapomorphies revealed in the analysis may be the consequence of too much noise in the matrix. In order to reduce the subjectivity as much as only the characters considered informative were included. However, I was finally probably misled, in the mechanical process to collect information, that the way to discover Hennig's hierarchy is simply to code every conceivable feature of specimens into a matrix, and expect that the parsimony analysis will find the congruence among these "close-to-random observations". This assumed that the right topology, even if the signal (i.e. any synapomorphies that might happen to be included) would be outweighed by the noise.

According to Platnick (2016), true congruence (e.g. between two or more authentic synapomorphies) can easily be overwhelmed and hidden by a sample with large noise content. To avoid this, any sizeable matrix with a limited number of taxa, it is justified to apply methods of character weighting that attempt to minimize the noise problem (Wheeler 1986; Goloboff et al. 2008; 2017).

PARALOGOUS GENES AND LONG BRANCHES

I was aware that one possible drawback of the use of some markers such as the ribosomal DNA genes was the possibility of divergent paralogous copies amplification which might confound phylogenetic reconstruction (Murphy et al. 2006; Vink et al. 2011). I checked the presence of multiple PCR bands and removed uninterpretable sequence chromatograms. Finally, sequences that produced obvious long branches on the trees (see Appendices 14b-17b and 20) were removed from the analyses. The phenomenon was frequently found among the two rRNA-gene trees (18S & and 28S) in Titanoecidae and some *Mallinella* species from Asia (Appendices 16b, 17b and 20). Paralogs or long-branch attraction can be problematic even in well-sampled groups of closely-related species, and use of maximum likelihood and multiple genes does not necessarily ensure estimating the correct topology under these conditions (Wiens 2004).

LACK OF PHYLOGENETIC RESOLUTION

We observed general lack of resolution in the morphological-based and molecular-based trees. However, we did not observed incongruent topologies between the different analytical methods on the major datasets. Although most of the genes taken separately did not recover the monophyly of Zodariidae (see Appendices 13-17), the partitioned multigene and combined data, or under morphology alone, did support monophyly of the family.

However, despite the strong support for the monophyly of the Zodariidae and the fairly well defined subfamilies in the multigene analysis, the lack of resolution within those groups is quite puzzling (Figs 10-14). The Storeninae is the only clade that is not supported by ML neither in the multigene, nor in the combined analyses. In a certain way this weakness is also, independently, reflected in the morphology-based tree, in which representatives of some Storeninae are scattered across the tree (Fig. 9, Appendix 7). Indeed, some of these taxa seem devoid of singularities that can define the subfamily, appearing plesiomorphic (e.g. *Antillorena*, *Cybaeodamus*, *Australutica*) or being strongly specialized (e.g. *Leprolochus*). Treating those kinds of taxa with the hope that a cladistics analysis based on parsimony and many characters will resolve the taxonomic placement is the main problem raised by Platnick (2016) concerning large matrix (see above) and thus not finding correct synapomorphies. In this case, the use of genetics for resolving these taxonomic uncertainties is obviously helpful.

When I started my study on the phylogeny of the Zodariidae in 2010, the set of molecular markers I used was essentially limited to the few that could be amplified across spiders (e.g. Hormiga, Arnedo & Gillespie, 2003; Hedin & Bond, 2006; Maddison & Needham, 2006; Rix, Harvey & Roberts, 2008; Spagna & Gillespie, 2008; Vink et al., 2008; Giribet et al., 2010; Miller et al., 2010). Then, the impulse for inclusion of a greater number of loci in molecular phylogenetic studies was provided, in part, by the inadequacy of genes like 18S and 28S for adequately testing family-level hypotheses on their own (Agnarsson et al. 2013; Kuntner et al. 2018). Until recently, the majority of molecular spider phylogenies relied on these relatively few markers. These did not often live up to their promises for recovering deep evolutionary inference, neither at the inter-familial nor at the sub-familial levels (Lopardo et al. 2011; Agnarsson et al. 2013; Wheeler et al. 2017; Kuntner et al. 2018).

It may be possible that old and, at the same time, rapid radiations in spiders mask the informative mutation points that have been overwritten by subsequent changes, leading to the difficulty to resolve unambiguously ancient splits in the spider phylogeny of that group. Recently, the phylogenomics and transcriptomics era is bringing spider systematics to a new level. Many questions regarding spider evolution are now addressed more rigorously, leading to detailed solutions (e.g. Garrison et al. 2016; Kuntner et al. 2018).

MORPHOLOGY TO THE RESCUE

The monophyly of the Zodariidae was supported by multigene, combined and parsimony analyses although the overall pattern of relationships among the family and sub-groups differed. Furthermore, probably a result of poor resolution at deep nodes within the Zodariidae, some taxa, such as *Procydrela,* have different position in the analyses using ML and BI approaches (compare trees on Figs 10 or 13 with Appendices 18 and 19). However, despite the wide range of homoplasies and the few synapomorphies revealed by the morphological analysis, the combined analyses, in which molecular and morphological data were simultaneously analyzed, provided a well-defined tree for which the support values of most nodes were reinforced. In this relevant tree, clades and taxa are fixed as consistent topologies both with Maximum likelihood and Bayesian approaches (Fig. 15).

CONCLUSION AND PERSPECTIVE

This PhD thesis aimed at the phylogenetic revision of the spider family Zodariidae. The discovery of numerous unknown taxa led to the description of new genera and species and the discovery of a peculiar, previously undocumented feature.

We have assembled and analyzed three large, separate datasets (morphology and multigene sequence data and a combination of both), of zodariid spiders and their close relatives, to provide the first total evidence phylogenetic analysis and the basis for a phylogenetic classification of the Zodariidae.

Very few synapomorphies were revealed in the morphological analysis, rendering the morphological diagnosis of some groups (e.g. Lachesaninae, Storeninae) particularly difficult. However, one possibility to get around this problem could be to map the characters on the total evidence tree disclosing more synapomorphies for the diagnosis of the monophyletic groups. Misidentifications of specimens were solved by reciprocal illumination. I also faced some difficulties in the coding of features in zodariid taxa, and was confronted to lack of resolution and conflict of signal (mainly for deeper nodes) between the morphology and the "molecules". However, the analysis with statistical methods of DNA + Morphology combined, surprisingly provided a higher support for most nodes in general and a stabilized tree topology. Six groups corresponding to six sub-families are recognized, even if relationships between them still remain to be tested by further studies.

It became clear to me that the future of the phylogeny and systematics of spiders at the family and beyond deeper level will be mainly dealt by genomics already in effervescence (e.g. Bond et al. 2014; Fernández et al. 2014, 2018; Garrison et al. 2016; Hamilton et al. 2016a; Maddison et al. 2017; Starrett et al. 2017; Kallal et al. 2018; Kuntner et al. 2018; Shao and Li 2018; Wood et al. 2018).

Genomics is likely to provide some outstandingly useful synapomorphies. According to Platnick 2016 "they are likely to be higher-order similarities, involving changes in gene order and expression, rather than low-level similarities among endless saturated, paralogous sequences of nucleotides, each of homology fully as dubious as the leg spines of spiders or scale counts of fishes".

A tenacious problem in such phylogenetic studies with genomics and transcriptomic approaches is the need of fresh/live specimens. The global biodiversity crisis induces additional challenges in this respect as taxa are disappearing before the can be sampled. Although nearly 50,000 spider species have been described to date, it is estimated that we have not yet discovered even half of the extant spider species (Agnarsson et al. 2013). With global climate change and habitat loss, the challenge will be to discover and describe species before they go extinct.

Despite many undeniable advantages of molecular data, it is still absolutely necessary that we continue to collect additional morphological data (on extant and fossil taxa) for systematic and phylogenetic analyses, and continue to improve our methods for morphology-based phylogenetics (Wiens 2004; Giribet 2015). Morphological data are indispensable for reconstruction of character patterns evolution (Wanninger 2015). Furthermore, most taxa described to date (not only spider species) are known only from a few specimens preserved for morphology rather than molecules (Agnarsson et al. 2013). It is still important to have rigorous, morphology-based phylogenies as a "reality check" for molecular results and vice-versa (Hillis and Wiens, 2000; Jenner, 2004; Wiens 2004).

Finally, although the impression may exist that morphology is overwhelmed by molecular data, it appears that the inclusion, in molecular analyses, of even a few irrefutable synapomorphies, can help to solve deeper nodes and improve the resolution of poorly defined molecular trees (Lopardo et al. 2011).

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